





AN INTRODUCTION TO
THE
MAMMALIAN DENTITION



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BY
T. WINGATE TODD,
M.B., Ch.B., Manc.; F.R.C.S., Eng.,
Captain, Canadian Army Medical Corps.

Henry Willson Payne Professor of Anatomy in the Western Reserve
University, Cleveland, Ohio; Formerly Lecturer in Anatomy
Victoria University of Manchester, England.

WITH 100 ILLUSTRATIONS

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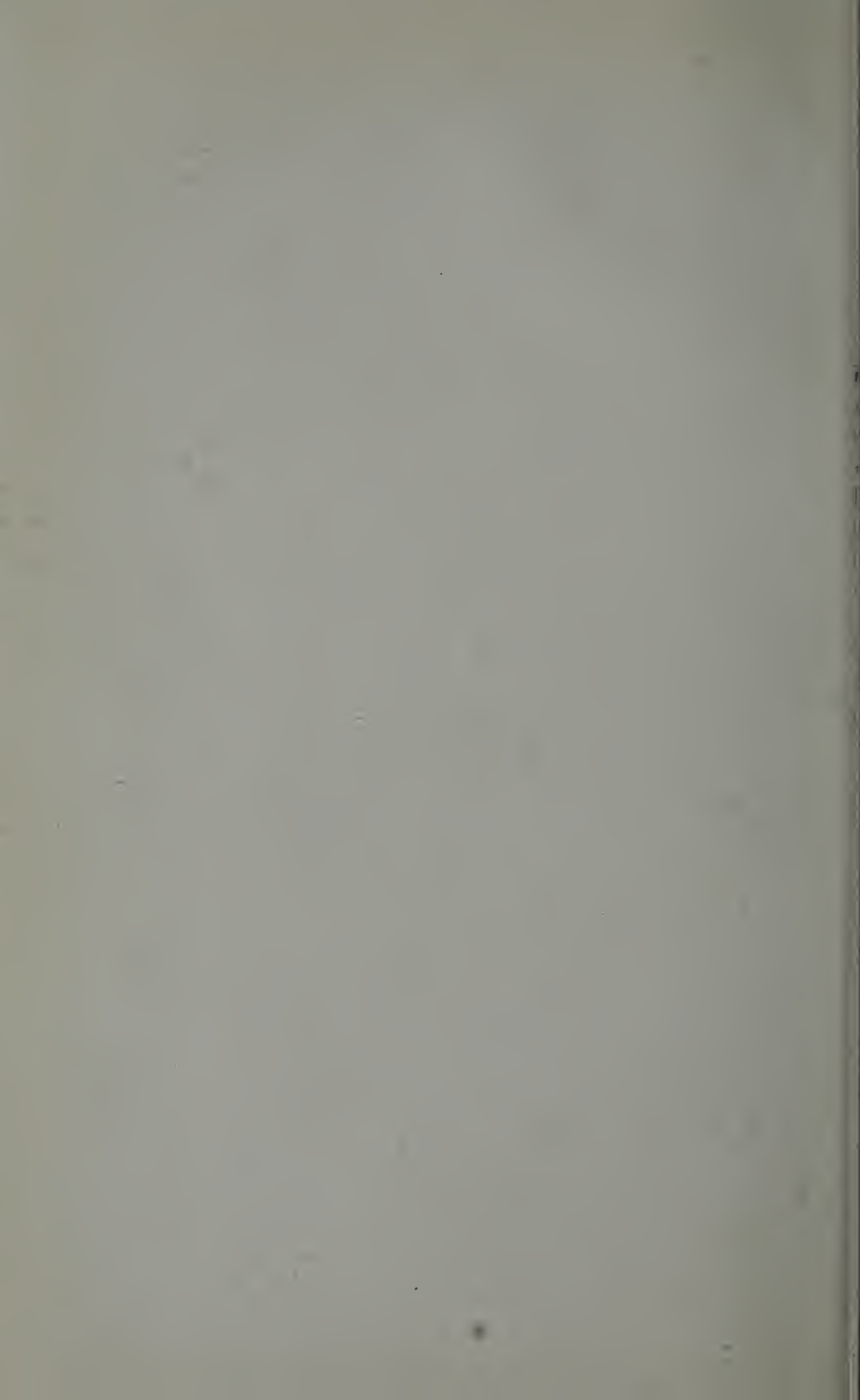
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1918

TO

DR. C. A. HAMANN

BY WHOSE UNTIRING LABOR THE FOUNDATIONS
OF THE WESTERN RESERVE ANATOMICAL MUSEUM
WERE LAID, AND BY WHOSE LAVISH GENEROSITY
ITS PRESENT COLLECTIONS HAVE BEEN SO LARGELY
BUILT UP.



PREFACE

In endeavoring to lay before my students truths embodied in the evolution of tooth form, I have been hampered as others undoubtedly have been by the relative inaccessibility of the essential literature. One cannot refer the undergraduate student to all sources of information with which one would like him to become acquainted. They are too scattered and too numerous to permit a student whose time is very limited and who is as yet only upon the threshold of the subject to glean those essential data which he ought to possess. From the profusion of material in the Anatomical Museum of Western Reserve University I have gathered typical examples of the various mammalian dentitions and have briefly presented these, allowing them for the most part to tell their own tale; for in the compass of so small a volume it is unavoidable that the writer's thoughts outstrip his pen and his conclusions lie often beyond the matter presented.

It has not been possible nor do I think it necessary to draw the attention of the reader to all theories and conceptions regarding the evolution of teeth. The views of Schwalbe and Bolk, for example, find no place within these pages. This is not because the writer has underestimated or brushed lightly aside the work of certain investigators. The volume has for its aim the presentation of essentially American views regarding the evolution of tooth forms, views which so far have not been made the basis of an introductory handbook. It is extraordinary that the Tritubercular Theory of Cope and Osborn in its more recent garb should find so small a place in the various treatises upon comparative anatomy of teeth. Now that facts in embryology hitherto regarded as incompatible

can be perfectly harmonized with the paleontological record there is, to the writer's mind, no reason for further hesitation in accepting as a fundamental basis of mammalian tooth forms the Cope-Osborn theory clothed in its most modern guise. All other interpretations have been made subservient to this and the reader's mind is not distracted by reference either frequently or fully to other views.

It has been the intention of the writer to illustrate three fundamental principles of life: the marvellous potentiality for adaptation exhibited by organisms in general through the continual creation of the absolutely new; the occurrence of adaptations always in one of several definite directions; the frequency of pause, reversal, or secondary progression, in other words the discontinuous character of evolution.

In every field it has been human fortune to discover first the laws of blood and iron, to gain an impression of irrevocable immutable implacable pitiless Force unsoftened by one touch of tenderness. Only with the fuller biological knowledge comes the vision that "if the courses be departed from, the ends will change" and further that the courses can be and constantly are departed from. One recalls how Claude Bernard's spirit revolted from the views current forty years ago when he wrote: "It is not by struggling against cosmic conditions that the organism develops and maintains its place; on the contrary, it is by an adaptation to, an agreement with these conditions. So the living being does not form an exception to the great natural harmony which makes things adapt themselves to one another; it breaks no concord; it is neither in contradiction to nor struggling against general cosmic forces; far from that, it forms a member of the universal concert of things, and the life of the animal, for example, is only a fragment of the total life of the universe." At this time when the soul of France typifies the spirit of emancipation from all that is hide-bound and cruelly inexorable, it is delightful to remember that Bernard's fellow-coun-

tryman Bergson has first applied the newer and grander biological interpretation to the philosophy of life.

The author recognizes that a Dental Anatomy course of today calls for the description mainly of living types which, however, can only be properly presented by constant reference to ancestral forms. Hence, although the following pages deal mainly with recent dentitions, the paleontological viewpoint has been adopted wherever it has been possible to do this without overburdening the text. To have elaborated more upon the paleontological aspect would have greatly increased the size of the volume and made it more than a simple introduction to the study of teeth.

In the preparation of this manuscript the author is indebted to many investigators who by personal contact or by their writings have influenced his thought. It is not possible to mention all by name, nor has it been thought advisable in so elementary a book to include a literature index.* To the late Professor A. H. Young, to Professor Grafton Elliot Smith and to Professor Arthur Keith I owe that debt of gratitude which can be acknowledged but never paid for my training in comparative anatomy. To Professor H. F. Osborn, Dr. W. D. Matthew and Dr. W. K. Gregory whose work has so greatly influenced me and upon whose writings I have so largely drawn I am happy also to declare my indebtedness. To Professor B. A. Bensley's work I owe the conception of the fundamental plan of this volume. For recent encouragement and the material resources with which the Anatomical Laboratory here is so richly provided I am under obligation to four gentlemen. Dr. Hamann my predecessor and colleague has spared no effort to acquire whatever has been necessary to equip the Museum with every advantage for the work. Mr. G. G. Marshall has provided us with a large collection of Ohio Mammals. The Hon. Newton D. Baker when Mayor of Cleveland and his indefatigable Com-

*A few selected references to recent literature upon the subject of teeth and allied problems mentioned in this volume are presented as an appendix upon page 282. This list is merely intended to refer the student who desires a wider acquaintance with the subject to certain original articles from which he will be able to obtain a more comprehensive view and an introduction to the literature.

missioner of Parks Mr. F. Alber placed the resources of the Cleveland Zoological Park completely at my disposal. To all these gentlemen I would gratefully acknowledge my indebtedness. Professor R. A. Budington of Oberlin and Mr. W. H. Cathcart of the Western Reserve Historical Society's Museum have shown me many kindnesses.

The great majority of the illustrations are photographs from specimens in this laboratory but for some I am indebted to the kindness of other writers. Figs. 57C and 80 are photographs of specimens loaned to me by Professor Budington from the museum of the Zoological Laboratory of Oberlin College. By Dr. Matthew's courtesy Fig. 1 is reproduced from his work *Climate and Evolution*. Fig. 2 is modified from Prof. V. Buttel-Reepen's work *Man and His Forerunners*. Figs. 3, 4 and 86 are from *Comparative Dental Anatomy* by Drs. Thompson and Dewey. Fig. 5 is from 'Tomes' well-known *Dental Anatomy*. Dr. Gregory very kindly made a modification of his Fig. 2 *Orders of Mammals* for incorporation as Fig. 8 of this work and also permitted me to copy Fig. 94 from his *Studies on the Evolution of the Primates* (Part I). Figs. 9, 10, 11 and 12B are taken from Dr. R. Broom's writings (see Appendix). Owing to war conditions it has been impossible unfortunately to communicate directly with Dr. Broom in order to secure from him an expressed willingness for the utilization of his figures. Yet I feel sure this permission would readily have been granted had it been possible to reach Dr. Broom himself. Fig. 12A is from the late Professor H. G. Seeley's monograph on *Diademodon* (Phil. Trans. Roy. Soc., 1894, vol. 185, p. 1029).

Professor H. F. Osborn and the Macmillan Company have kindly allowed me to reproduce Figs. 13 and 14 from *Evolution of Mammalian Molar Teeth*. Figs. 15 and 16 are obtained through the courtesy of E. S. Goodrich, Esq., and J. W. Gidley, Esq., respectively. On account of the transportation difficulties then affecting the United States the works (noted in the Appendix) of these two gentlemen from which these figures were

originally taken were inaccessible to me at the time when I was completing the list of illustrations. I am therefore indebted to Professor Osborn and the Macmillan Company for the opportunity of copying the reproductions of these two illustrations from *Evolution of Mammalian Molar Teeth*. It will be observed that the mandibular molar in Fig. 15 was redrawn for Professor Osborn's work; this accounts for the differences in nomenclature from the original figure. For the specimens from which Figs. 56A and C were made I am indebted to Dr. M. J. Cramer and Mr. B. H. Broadbent respectively. Professor Keith has kindly allowed me to reproduce from his works Figs. 59 and 98. I have the opportunity to include Fig. 84 through the courtesy of Oldfield Thomas, Esq. Fig. 87 is copied from Dr. Otto Walkhoff's monograph *Der Unterkiefer der Anthropomorphen und des Menschen* in the late Professor Selenka's series *Studien über Entwicklungsgeschichte der Tiere*, heft 9.

I have enjoyed the assistance of several of the departmental staff in the preparation of this work. Mr. G. P. Leonhart has prepared a number of the specimens many of which have been photographed by Miss Alice Thing. The index is largely the work of Miss W. Rothenbecker. I am under special personal obligation also to my secretary Mrs. K. W. Merrell for many suggestions made in the course of writing the manuscript as well as for the technical preparation of the sheets for the press.

T. WINGATE TODD.

Cleveland, Ohio,
Dec. 1, 1917.

The transformation of the United States into an armed camp, heartening and inspiring to all who have been privileged to live in the midst of it, has been responsible for unforeseen delay in the publication of this volume. One after another those by whose joint labor the book should have been produced months ago have taken up other duties in the cause for free-

dom. It has also provided the author with the welcome opportunity of putting to practical application lessons learned in hospital and laboratory during the last decade concerning the generation and regeneration of bone. I am happy therefore to acknowledge my indebtedness to Dr. N. W. Ingalls for undertaking to see this manuscript through the final stages of the press.

T. W. T.

Carling Heights Military Hospital,
London, Ontario.
May 24, 1918.

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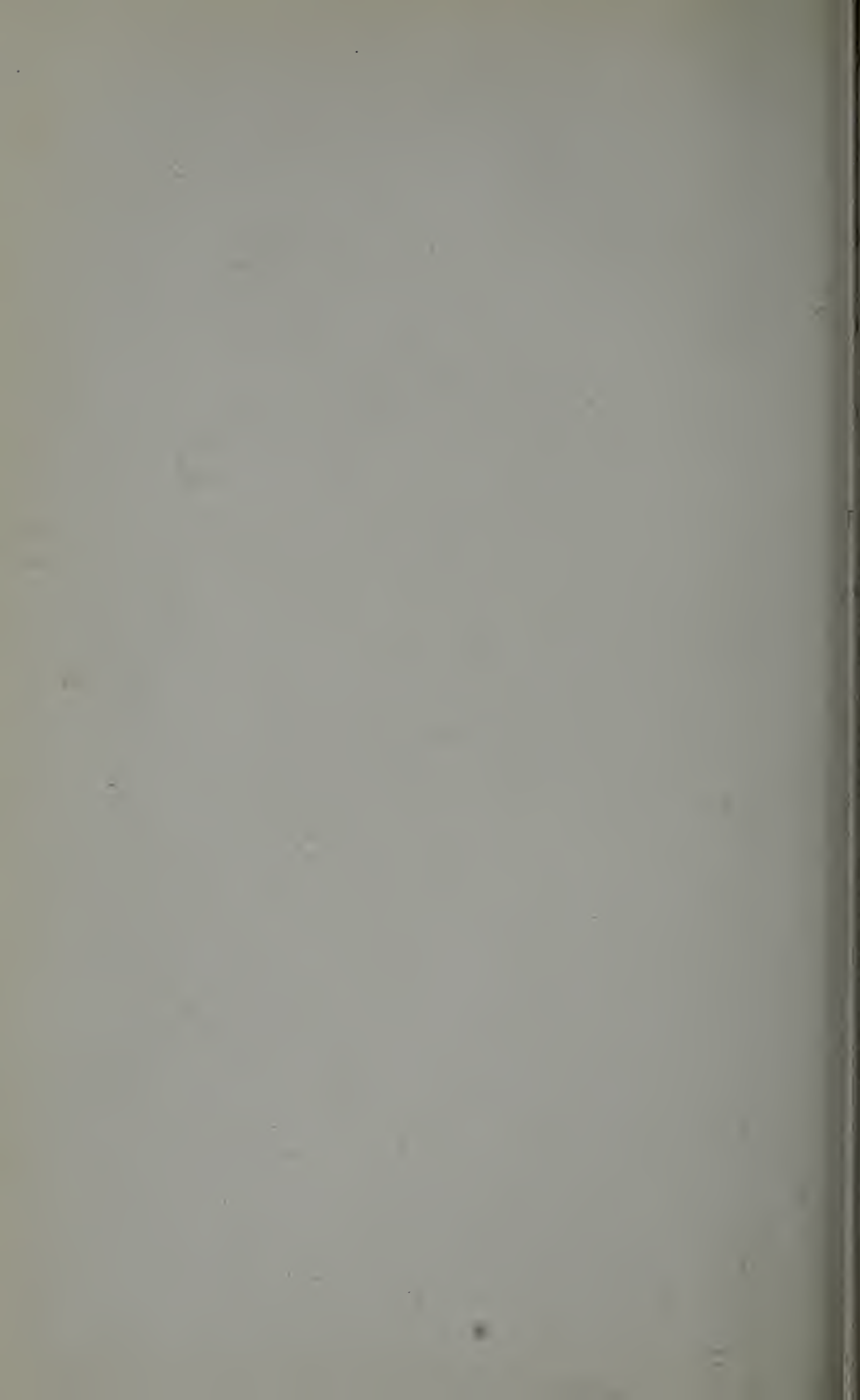
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MAMMALIAN DENTITION

CHAPTER I

ENVIRONMENT AND THE EVOLUTION OF VERTEBRATES

The relation of Man to other Mammals—Geological changes since the first appearance of land vertebrates—Influence of the division of land masses upon animal evolution—Preservation of bones and teeth—Relation of climate to evolution and migration—Definition of evolutionary terms—Variations and mutations.

That which fires the imagination, which encourages us to follow all the devious paths of mammalian tooth development in the study we are undertaking, is the evolution of ourselves. Our chief interest naturally centers around our own dentition. When we come to ask ourselves what characters of really fundamental importance differentiate us from other animals we find these are singularly few. The perfection of the erect posture, the power of speech and the great increase in the parietal association area of the brain separate us perhaps most clearly from even our nearest animal relatives. Other features such as size and certain characters of the teeth are by no means confined to our own particular history; they are shared in common with other animals. We cannot isolate ourselves from our nearest mammalian kin with which we are classed in the order Primates.

If in the attempt to trace our own history we follow back the ancestors of the Primates to their earliest beginning we

find ourselves already at the parting of the ways where the various orders of Mammals diverge. We must then realize that all Mammals are members of one great tribe and that we cannot consider the origin of one family or even of one species without referring eventually to the ancestors of others.

Mammalian history covers a colossal period of time. Not a century, not a millennium but eons are occupied in the evolution of the mammalian class. During this period incalculable in



Fig. 1.—Zoological regions on north polar projection. (After Matthew.) The unshaded areas around the continents indicate the extent of the continental shelf and thus show the greatest possible land connections permitted by the theory of Isostatic Balance.

human thought the earth has seen considerable changes; periods of heat and cold have followed each other; the ground has sunk beneath the sea and risen again above it; yet, and this is very important, the main confines of land and water in all probability have remained approximately the same. If one turn to an ordinary map of the world on Mercator's pro-

jection the intimate relation to each other of the land surfaces is not apparent. Indeed from a zoological standpoint this map is useless. On the other hand if one look at a map on north polar projection (Fig. 1) one sees immediately that Asia and America are closely related across the Bering Strait and also by way of Europe and Greenland. Nowhere is the sea deeper than some 600 feet. If, therefore, the land were raised by this amount there would be actual continuity between these various land masses and animals would be free to roam from one to the other provided the conditions of climate were not unfavorable. Very different is the case in the southern hemisphere. Around Antarctica is a sea of great depth separating this land from Australia, South Africa and South America and also isolating these various land masses from each other. No gentle undulation, no slight rise of the earth's surface could obliterate this sea. It is doubtful if these land masses have ever been connected; if animals could pass from one to the other at any time except across the ocean.

The alternate rise and fall of the land with consequent withdrawal and encroachment by the sea is known by the term *Isostatic Balance*.^{*} Around each continent, extending under the sea for a variable distance, is the *continental shelf*. The mountains and the higher lands are constantly washed away by river action or by glaciers and the sediments deposited in the shallow water upon the continental shelf. Thus land is formed at the mouths of rivers, being transported from its original situation in the interior. The weight of this made land is supposed to have some influence in causing the crust of the earth beneath it to sink and in consequence to bring about the elevation of the land remote from the coast. Whether or no this theory be justifiable we know at least that land is constantly removed and as constantly raised anew. With these

^{*}It is beyond the province of this volume to consider the arguments in support and in controversion of the vexed theory of Isostatic Balance. Those who are specially interested in the relation of this theory to the problems of mammalian evolution and migration cannot do better than study carefully the papers by Matthew: *Climate and Evolution*, Ann. New York Acad. Sc., 1915, xxiv, 171; and Barbour: *Some Remarks upon Matthew's "Climate and Evolution,"* Ann. New York Acad. Sc., 1916, xxvii, 1.

changes of alternate lowering and raising of the earth's surface the climate changes. In general a low marshy ground possesses a warm equable humid climate; a high plateau induces a cold variable and arid climate ultimately ending in glacier formation. The character of the land and the nature of the climate are intimately associated with each other.

The continents have joined and separated again in the regions already indicated not once but several times; most islands also have varied in their relationship to the adjacent greater land masses. Britain and Japan are comparatively young islands; they have not been separated from the adjacent Eurasiatic continent long enough for the production of marked insular changes in the types of animal life occurring upon them. Madagascar on the other hand has not been connected with Africa since the life time of the early Mammals and we find in consequence that the modern fauna of this island differs very considerably from that of the neighboring continent. New Guinea and Australia form portions of a still older island: between the Australasian archipelago and the furthest extension of the Oriental Region represented by the islands of Java and Borneo, there lies a channel of deep water formed by the Strait between the islands of Bali and Lombok and by the Macassar Strait separating Borneo from Celebes. This barrier of water is known as Wallace's Line and it has been said that no land has ever bridged across this channel since before the time when Mammals of modern type came to be. It is doubtful however if this statement should be accepted in the light of modern investigation. The fauna of Celebes is difficult to harmonize with the view that the island has been entirely separated from the Oriental Region for so long a period. Many authorities now believe that Wallace's Line has never existed except in theory. It is certain however that the modern type of placental Mammals with but few easily explained exceptions, never penetrated Australia and the neighboring islands until taken there by Man. With the foregoing exceptions the only Mammals found in the great Australasian archipelago are the

pouched creatures known as Marsupials. Animals similar to these in essential respects once ranged over the rest of the world but long ago, being less adaptable to the changing environment, became extinct and were replaced by the rising group of placental Mammals. In Australasia the Marsupials still remain relatively unhampered until recent years by the annoyance of powerful rivals. New Zealand has been an island since before the time when Mammals first appeared and none existed there until brought by Man. There are then two types of island, continental like Japan and oceanic like New Zealand; upon the former we expect to find a fauna very similar to that of the neighboring continent whereas upon the latter the animal life will have developed special local adaptations or peculiarities. The connection of an island with a neighboring continent has an important bearing upon the nature of its fauna. If the intervening sea is shallow its breadth is unimportant; if it has been recently nonexistent there will be no marked difference between the island fauna and that of the main land; if the sea has existed for a great period of time independent evolution will have taken place in the island fauna and great differences between it and the continental animals will now be apparent.

The anatomy of animals which are now extinct and the history of those which still roam the earth are naturally studied mainly from the bones and teeth, the indestructible portions defying time which are transformed into fossils. These are the skeletons of creatures which have fallen into swamps, into marshes or occasionally into asphalt pools and dying there have been preserved. They are the skeletons of animals overwhelmed by dust or snow storms and buried. Occasionally an animal has been overtaken by the ice, frozen into a glacier and in this manner preserved until the glacier has melted. Early in the present century we heard of wolves glutting themselves upon the carcass of an age-dead Mammoth newly released from a melting glacier, before the animal was obtained for the Petrograd Museum. The Russian steppes are today occasionally

the scene of the extermination of vast herds of cattle or sheep in a blizzard; the camels which wander half wild amid the ruins of Asiatic towns are probably the descendants of those domesticated animals surviving the dust storm in which their owners perished. In such several ways are preserved the relics of ancient faunas but rarely are they undisturbed; the action of rivers and still more that of glaciers has cleaned from the slate of history many of the poor remnants that remained and not once but many times has the slate been cleaned since Mammals first appeared.

In the more northern part of Europe, Asia and America we must not expect to find deposits of animal remains in such profusion as in the regions further south which have not been exposed to glacier action. The southern continents of Africa and South America have been stated to be the great primary centers of mammalian distribution on account of the quantities of fossils preserved there in deposits of all geological epochs since the first Mammals appeared. They may have been secondary centers but it is altogether doubtful if Mammals originated upon either one of them.

The relation of climate to evolution and to dispersal of animals is most important. If we note the periods of alternate cold and warmth we find that it is in the former alone that great strides are taken by animal life. In the accompanying table (Fig. 2) it will be observed that it was during the glacial phase of the Devonian period that land animals in the form of Amphibia first appeared. Again during the cold stage of the Permian we note the rise of Reptiles and probably the first beginning of the mammal-like creatures. On the other hand during the warm moist Jurassic epoch we find the Amphibia which have by this time evolved into a very numerous group decadent and already disappearing. The Reptiles, a vast and miscellaneous host, some of them stupendous in size, begin to disappear during the Cretaceous period which included a warm moist stage sandwiched between two glacial phases. During this epoch we note also the rise of archaic Mammals which be-

	Names of Strata	Approximate thickness of Strata	Duration of periods (minimum estimate in years)	Alternations of Climate	Effect upon animal life.
{Quaternary Cenozoic	{Recent: Pleistocene (The Glacial Period)	{3,000 feet	3,000,000	Arid	Rise of modern Mammals.
	{Pliocene				
	{Miocene				
	{Tertiary	{Oligocene Eocene (Including Paleocene)	{10,000 feet	11,000,000	{Warm, uniform Arid Warm, uniform Arid (at beginning)
{Cretaceous Jurassic Triassic					
{Secondary (Mesozoic)	{Permian Carboniferous	{50,000 feet	34,000,000	{Arid Warm, uniform Arid (towards end) Warm Arid	Rise and early differentiation of Reptiles. First adaptation of Vertebrates to terrestrial life—Amphibia. First appearance of Fishes.
	{Devonian Silurian Cambrian				
{Archeozoic	Precambrian	100,000 feet	52,000,000		

Fig. 2.—Table of Geological periods. (Modified from Buttel-Reepen.) The table indicates the type of climate in the several periods and the rise and disappearance of the vertebrate classes excluding Birds.

came especially numerous during the warm moist Eocene and then gradually gave place to modern types of Mammals which evolved during the cold Pleistocene known usually as *The Glacial Period*.

From the foregoing it is apparent that periods of cold have a stimulating influence upon animal life whereas warm equable climates by their enervation result in deterioration and final extinction of the type. Extermination is preceded by increase in size and by lethargy; this is natural since it is easier to obtain food as a rule in a warm climate and life is much less strenuous. In the colder environment the animal must be alert and vigorous to maintain its existence. In some obscure manner climate has a marked influence upon the evolution of different types in adaptation to the ever-changing environment for we note the successive dominant types Amphibia, Reptilia and Mammalia.

Intimately associated with the environment is the dispersal of animals. It stands to reason that a creature which is not capable of changing its life habits to suit its changing circumstances must migrate when the climate changes in order to follow the receding warmth and maintain an unchanged environment. Paleontology shows us that these migrations have usually been from north to south exactly as we would expect since we have observed that it is the cold phase which stimulates progressive evolution.

Before going further we should differentiate clearly between the terms primitive, generalized, advanced, and specialized as applied to Mammals. A primitive animal is one which has retained many of its ancestral or archaic characters; it may be very specialized but it cannot be generalized nor can it be advanced. A generalized animal may be primitive and usually is in some respects; it is not specialized because it retains the ability to change its life habits with changing environment. An advanced animal may be generalized or it may be specialized but it will not be primitive; it has changed greatly from the ancestral type. A specialized animal may be primitive or ad-

vanced but it has lost its power of adaptation to changing environment and is therefore not generalized.

We wonder in what manner changing environment has influenced the evolution of the vast number of mammalian types which exist or have existed on the face of the earth. The most closely related species are not found living together; they will always be separated by some barrier of mountain or water. In species formation it is usual to consider at least four aspects,—variation, heredity, selection and segregation* of which the last has already been touched upon. Regarding variation it is necessary to define the term more precisely. Those variations which are heritable are known as mutations. Obviously there can be three types of mutation, those without effect upon the relation of the animal to its environment, those which produce a type less in harmony with its environment, and those which render it in closer harmony. Of these the persistence of the first is accidental; animals exhibiting the second must ultimately become extinct by the action of natural selection; those in which the third type of mutation occurs become dominant and persistent. Segregation permits of the independent evolution of mutations which we shall eventually find occur linked in vast numbers appearing always in certain well defined directions through the inherent tendencies of the germ-plasm. We are concerned in this book with those mutations only which are of importance in the relation between the animal and its environment.

We are indebted to Waagen, an Austrian paleontologist, for

*It must be conceded that these aspects differ greatly in complexity and the meaning of all except the fourth varies according to the concept of the writer. Of them segregation is simply one environmental factor; selection is not creative, but in Osborn's metaphor a sieve for the results of interaction of environment (animate and inanimate surroundings), ontogeny (laws and forces operating in the development of the individual) and heredity (laws and forces operating in the germ-plasm); variation is the expression partly of environment, partly of ontogeny as just defined, partly of heredity. Further there is interaction of which we are as yet utterly ignorant between the forces of heredity on the one hand and those of environment and ontogeny on the other. The initiation of new characters is not the special perquisite of any one of the three factors environment, ontogeny, heredity, but is common to all. Thus upon closer examination it is seen that the four terms used in the text, though apparently simple enough, are really the expression of considerable confusion of thought. The unknown agency which works through heredity and is termed by Bergson the *original impetus*, we shall discuss in Chapter XXI. For further information along these lines, consult Osborn: *Tetraplasy*, Jour. Acad. Nat. Sc., Phila., 1912, series 2, xv, 273

first pointing out the transformation of one form of animal into another. Ten years after the publication of Darwin's *Origin of Species* Waagen showed that minute and inconspicuous changes of form occur constantly in the history of a race. These changes which he called mutations are heritable and gradually accumulate in successive generations until they become recognizable. The most important of Waagen's observations was that these accumulations of mutations occur always in definite directions. This means that there is a certain limited number of types of response which it is possible for the germ-plasm to exhibit. That these responses are adaptive has been clearly shown by Osborn. One scarcely likes to use either of the terms *ordered response* or *choice of response* in this connection because of the anthropomorphic significance which these phrases have come to possess. The former suggests a creative plan and the latter a mentality on the part of the organism by no means implied in these pages and carrying us further into the realm of philosophy than we can go in this volume. We cannot expect to understand why the germ-plasm should respond in a particular manner until we attain more complete knowledge than we have today of the interaction of the forces of heredity with the various factors composing the environmental stimulus. Throughout the succeeding pages, however, the reader will find in the evolution of teeth ample evidence of limited and definite *types* of response comparable with those to which attention was first drawn in Invertebrates by Waagen.

CHAPTER II

THE DENTITION OF LOWER VERTEBRATES

The relation of teeth to scales—Attachment of teeth—Teeth of Fishes, Amphibians and Reptiles—Evolution of “cusps”
—The pronounced development of certain teeth.

Teeth as popularly understood may be defined as calcified papillæ of the skin secondarily implanted in the bones of the jaws and subserving the purpose of mastication. That this is but a crude conception will appear upon the slightest reflection for it is based only upon certain generally recognized features of our own dentition and one cannot think for a moment that our teeth sprang into existence fully formed and adapted at once to their present function. It is indeed only after a long period of evolution, of constant modification and adaptation to circumstances that the present form and characters of our teeth have developed. To understand even our own dentition intelligently it is necessary to trace it back to its earliest beginning and to follow carefully the successive steps by which it attained its present condition. Upon discussing our definition more in detail we shall find that it becomes merely a generalization more or less exact and of limited applicability.

If we examine the jaws of a Dogfish or Shark (Fig. 3) we shall observe that the horny scales of the skin are continued over the framework of the jaws into the mouth and that on the rounded surface of the jaws these scale-like structures assume the form of simple triangular teeth in successive rows. Hence we shall be less surprised at the suggestion that the teeth are in reality modified dermal appendages. But if next we take the head of a Pike (Fig. 4) we do not see this simple transition and further we note the appearance of small but distinct tooth struc-

tures upon the walls of the pharynx and the branchial arches beyond the limit to which Embryology has taught us the external skin has penetrated. It is plain then that teeth cannot in



Fig. 3.— Jaws of Shark to show formation of simple triangular teeth from dermal scales.
(After Dewey-Thompson.)

every case be dermal in origin but may sometimes develop from the surface layer of the alimentary canal itself. Thus we see that structures finally similar may in the beginning arise in quite different manner from dissimilar tissues.

The very fact that we have chosen fish in this first illustration indicates that the occurrence of teeth is by no means confined to the higher animals. Analogous structures have indeed been found in some Invertebrates but it would not help our present purpose to consider these. We must note however that teeth of a simple pattern exist far down in the vertebrate scale.



Fig. 4.—Jaws of Pickerel to show the occurrence of teeth upon the palate. (After Dewey-Thompson.) Teeth are not confined to the jaws themselves.

Another point to notice is that whereas the teeth upon the jaws of the Pike are firmly united to the underlying bone those of the palate are hinged so that they can be made to lie flat against the buccal lining, their tips pointing toward the throat, by small fish as prey passing through the mouth. If however

the small fish should attempt to wriggle out again and resist being swallowed, its backward movement causes these palatine teeth to rise and form a forest of spears whose points are all directed toward the throat, effectually preventing the escape of the victim. The attachment of teeth to their foundation is by no means uniform and although we are accustomed to think



Fig. 5.—Section of palatine tooth of Pike (*Esox lucius*). (After Tomes.) The hinged character of the attachment to the underlying bone is shown. This permits change in position of the tooth.

of teeth in Man and all Mammalia as socketed in bone yet in lower forms teeth may be attached to underlying tissues in one of several ways (Fig. 5). In Sharks indeed the teeth are not fixed to the underlying jaws at all but simply held in place in the integument.

Very few fish can be said to masticate their food even in

limited degree and hence once again our generalization falls short of completeness. Many Mammals, the domestic Cat among them, use their teeth only for seizing and dividing their prey not for masticating it. Teeth are then in the first place prehensile organs and only later become modified for dividing, crushing or masticating food. For the mere seizing and holding of prey the conical teeth seen in many fish are perfectly satisfactory and it is with such simple forms that our study must commence.

The numerous modifications of form, structure and attachment of teeth as exemplified by Fishes have no immediate concern for us since our object is the investigation of the mammalian dentition and we may therefore pass on at once to consider teeth in higher forms.

On an evolutionary plane higher than that of the Fishes we find the now specialized and aberrant group Amphibia which includes the Frogs, Toads, Newts and Salamanders. Upon examination the upper jaw of the Frog shows a row of small conical teeth firmly ankylosed to the underlying bone and projecting but little from the surface of the soft tissues lining the mouth while the lower jaw is edentulous. There are other teeth upon the palate, the so-called vomerine teeth, also simple and small but we shall not stay to consider them. The Frog is not limited to one set of teeth alone; successional teeth originally developed at the inner aspect of the older teeth eventually undermine the bony pedestal of the last mentioned and complete their development in what was originally the pulp cavity of their predecessors, ultimately being fused with the bony tissue precisely as are the teeth on the jaws.

Higher in the scale than Amphibians are the Reptiles which comprise Lizards, Snakes, Turtles and Alligators. All of these have become specialized although the Lizards perhaps less than the rest. But all modern Reptiles are far removed from the main evolutionary track which we intend to follow. Nevertheless among them are to be found many interesting modifica-

tions of tooth structure one or two of which may be mentioned as of special significance for our purpose.

The jaws of the Iguana (Fig. 6) show an experiment of Nature in producing a type of tooth somewhat more complicated than the simple cone. Careful examination of these shows that most have not one single point or tip but several, often seven in fact, of which the central one is the largest and the most prominent. We see then that by very little modification a

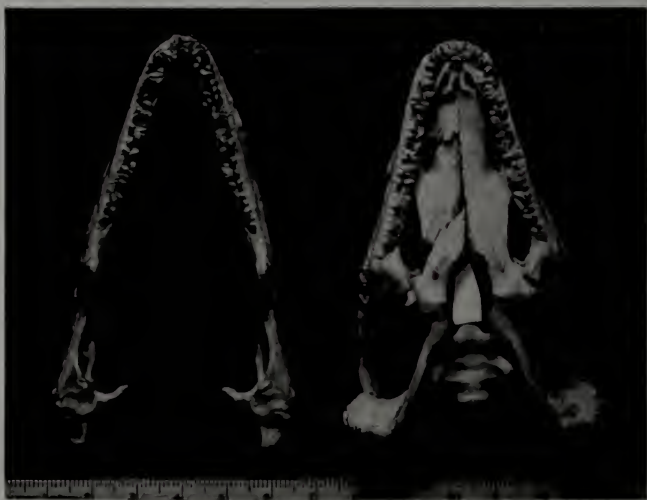


Fig. 6.—Jaws of Iguana (*Iguana tuberculata*, 81.1.1). This is an experiment of Nature in producing teeth with more than one tip or cone. The simpler teeth are those in the front of the mouth; the more advanced occur further back near the areas of muscular attachment.

tooth with many tips can originate. A further point which is worth our careful attention is that in the Iguana the teeth near the front of the mouth and below the nostril retain almost without exception the simple conical form. The more complicated teeth in this animal are most numerous further back on the jaws near the areas of muscular attachment.

The skull of the Mississippi Alligator (Fig. 7) shows that certain teeth may consistently grow to a greater size than

others. In this specimen the third and ninth in the upper jaw and the first, fourth and eleventh in the lower have attained greater size than the rest. The young Alligator when just hatched has as many teeth as the adult but the teeth are replaced from time to time by successors. Nevertheless, at whatever age the animal be, on examination it will always be found to possess these particular teeth larger than their fellows.

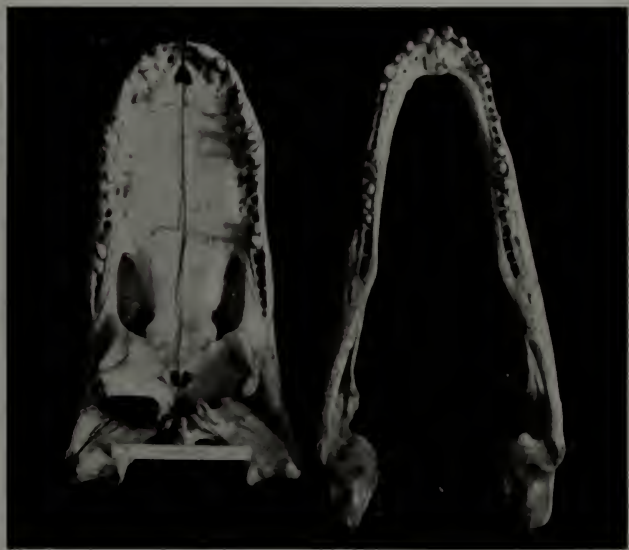


Fig. 7.—Jaws of Alligator (*Alligator mississippiensis* 81.4-1). The teeth are implanted in bony sockets and certain teeth are constantly larger than others.

A character again exemplified in the Alligators but not in other Reptiles is the implantation of the tooth into a socket. The tooth itself like that of the Mammal consists of dentine with a cap of enamel on its projecting surface and a sheathing of cement around its implanted portion. Though the teeth of the Alligator resemble those of the Mammal in possessing sockets in the jaws they are not strictly comparable for whereas the socket in the case of the Mammal is produced by

the growth of the tooth itself its occurrence in the Alligator precedes the eruption of the tooth.

The Reptiles form a large and miscellaneous assemblage of creatures but their most numerous and more primitive representatives are extinct. We must not expect to find among the living examples of this class the types which will interest us most. In fact the Reptiles may be subdivided into primitive, mammal-like and bird-like forms, of which all the first and second groups and many of the third are extinct. Modern Reptiles are all more or less closely allied to the Birds and it is interesting to note that the teeth in many of them, the Turtles for example, have been replaced by horny coverings for the jaws as in Birds. We now know that several at least of the ancestral forms of Birds possessed truly reptilian teeth.

A rapid survey has shown us the following suggestive facts. Teeth already occur in the lower vertebrate forms. They are at first simple conical outgrowths of surface epithelium which may or may not be attached in one of various ways to the underlying jaw. In higher forms the projecting part or crown may become subdivided into more than one point and this subdivision is liable to occur with greater frequency in the teeth situated on the jaw near the areas of muscular attachment rather than in those located near the middle line in the front of the mouth. Certain teeth, as shown in the Alligator, become larger and more powerful than the rest and these characters are also shared by the replacing teeth. Lastly the imbedded part or root of the tooth becomes implanted secondarily in a socket in the jaw bone. With these observations in mind we are now ready to commence the study of the origin of the mammalian dentition itself.

CHAPTER III

THE ANCESTRY OF THE MAMMALIA

Geological dawn of mammalian life—Differences between Reptiles and Mammals—Origin of mammal-like Reptiles—transformation of the limbs—development of the brain in mammal-like Reptiles—Cynodonts—Protodonts—Multituberculates—Triconodonts—Trituberculates—the parent form of mammalian teeth.

In the present volume the study of mammalian teeth is the essential object. By comparison of tooth forms zoological relationships of the various Mammals and of Man will be indicated. To institute comparisons of real value we must have a standard and this standard will necessarily be the primitive type of mammalian dentition. It is obviously futile to search for parent or stem forms among the considerably specialized Mammals existing today. Even among the remains of extinct Mammals ancestral to and simpler in form than those now living it is unlikely that the actual parent form* will be found although the fossil Mammals of an earlier day may be expected to show indications more or less clear of what that parent form must have been. Our search for indications of the features of this dawn type of Mammal must then be among the fossilized faunal relics of earlier geological periods.

With the exception of such rarities as the imprisonment of entire Mammoths in the ice fields of Siberia and the preservation of portions of the skin of gigantic Ground Sloths in the caves of Patagonia the only vestiges of extinct Mammals left to us are teeth and bones. Scarcely ever is a skeleton found complete and very frequently the component bones themselves

*Presuming, as is probable, that all mammalian orders had a common ancestral stem form.

are broken. Often there is merely a portion of a limb or a mandible exhibiting an imperfect complement of teeth, a fragmentary skeleton on which to base our reconstruction of the animal to which it once belonged.

If then the rocks hold the secret of mammalian ancestry, in what geological stratum may we expect to find it. Some authors have conceived the history of Mammals reaching to very early times but it appears probable that we need penetrate no further into the geological past than the Permian epoch to attain our goal. Examining in succession the Mammals of former periods, receding always further into the dim and more imperfectly known ages of the world's history, or even comparing the more primitive members of the mammalian class existing today with those more advanced, we note the occurrence of reptilian features more pronounced and more numerous the more primitive the type. From this fact we realize that Mammals must have been derived originally from reptilian forms although from forms very unlike those Reptiles which exist in modern days.

There must have been a time when certain creatures were transformed from the cold to the warm-blooded type and with this change the Mammals first appeared. Similar transformation of a different group of Reptiles brought about the origin of Birds to which rather than to Mammals all modern Reptiles are related. The story of the Birds however lies beyond our present scope.

It is true that the organization of a Mammal differs very greatly from that of a typical Reptile but in this account it is unnecessary to deal in detail with the characters of the body as a whole. We shall confine our attention to a few points illustrated by the dentition and the skull (Fig. 8). The mammalian mandible is constituted by a single bone* the representative of the reptilian dentary. The mandible in the Reptile on the contrary is more complex and is formed by several elements.

*Although the angular and surangular are not usually recognized many Mammals show a mere rudiment of the former and Ornithorhynchus possesses vestiges probably of both.

Of these the dentary bears the teeth; the angular and surangular lie near the hinder end; the articular forms a joint with the quadrate bone of the skull, a bone which has disappeared as such in the Mammal; the splenial lies upon the inner side of the dentary. Not only does the mammalian mandible differ from that of the Reptile in consisting of a single element but the

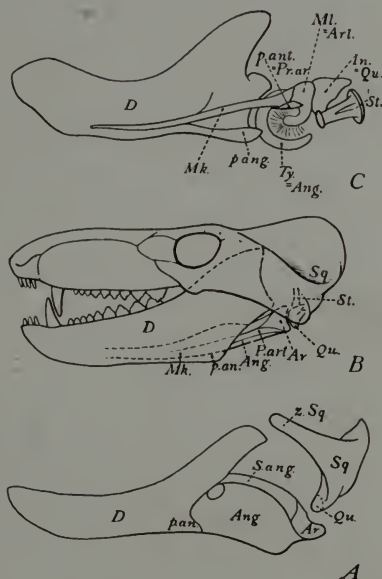


Fig. 8.—Morphology of the Mandible and Auditory Ossicles (after Gregory,* Orders of Mammals. Bull. Am. Mus. Nat. Hist., 1910, vol. 27, fig. 2, p. 124).

A. Mandible of a Permian Therocephalian (*Lycosuchus vanderietzi*, after Broom). Ang., angular; Ar., articular; D., dentary; p.an., processus angularis; Qu., quadrate; S. ang., surangular; Sq., squamosal; z. Sq., zygomatic process of squamosal.

B. Skull and mandible of *Cynognathus platyceps* (composed from figures by Broom). Abbreviations as in A. Mk., Meckel's cartilage; P. art., prearticular (Williston, i. e., the dermal medial extension of the articular); St., stapes.

C. Developing mandible and auditory ossicles of Kangaroo (*Macropus*, after Bensley).

Abbreviations as in foregoing. In., incus; Ml., malleus; p.ant., processus anterior mallei; Pr. ar., prearticular; St., stapes (turned back); Ty., Tympanic ring.

articulation of the bone with the skull is essentially dissimilar. In the Mammal the articular and quadrate disappear as such,

*This illustration has been modified by Dr. Gregory since the publication of his monograph, *The Orders of Mammals*, from which the figure was originally taken. By kind permission of Dr. Gregory the most recent modification of the figure is here reproduced.

possibly to become auditory ossicles the malleus and incus respectively,* and the dentary itself forms with the glenoid fossa on the squamous temporal a new and secondary articulation which tends to lie above the plane of the cheek teeth and not at or below their level as in Reptiles. In the Alligator some teeth project more than others although all are alike in shape. In the earliest Mammals it is always the first maxillary tooth which takes on a caniniform character, the incisors are relatively simple and the postcanine teeth become increasingly complex backwards. Whereas all reptilian teeth possess only a single fang, the roots of the cheek teeth and occasionally of the incisors and canines in the Mammal are subdivided.

In the skull as in the jaws we shall refer only to certain features of special present significance. In the Reptile the anterior nares are completely surrounded by bone; in the Mammal they are not. The reptilian condition is largely due to an upgrowth of bone from the premaxilla forming an osseous nasal septum to which is attached the *egg tooth* utilized by the hatching Reptile for the purpose of chipping open the egg.† In Mammals the orbit is separated from the temporal fossa by the postorbital process of the frontal and not by a special bone, the postorbital, as in Reptiles. The temporal fossa and coronoid process of the mandible providing attachments for the temporal muscle, and the zygomatic arch and ramus of the mandible for the attachment of the masseter are well developed in typical Mammals. The hard palate in the Reptile is formed by the premaxillae alone so that the posterior nares open into the mouth. In the Mammal on the other hand the horizontal processes of the maxillary and palate bones forming a septum between mouth and nose and thus forcing the latter to open into the pharynx, constitute the so-called secondary hard palate behind the incisive or anterior palatine foramen.

*It must not be supposed that all writers are in agreement concerning the fate of these elements. What we do know is that the elements disappear as such. The malleus, incus, tympanic ring, interarticular cartilage of the temporo-mandibular joint and even the zygomatic process of the squamous temporal have been claimed as representing the quadrate.

†This bone is represented in the young Monotremes and, according to Broom, in the young of some Marsupials (*Macropus*, *Trichosurus*).

The mammalian skull shows two laterally placed occipital condyles whereas the Reptile possesses a single median condyle ventral to the foramen magnum.

During recent years Dr. Broom and Mr. Watson have given much attention to the subject of premammalian Reptiles and the former has summarized in a tentative but attractive manner various features of the probable evolution of Mammals. We owe largely to Broom the elucidation of a group of fossil carnivorous Reptiles found in South Africa and belonging to Permian and Triassic times. In the earlier period the Therocephalia alone were present; in the Triassic the Cynodonts also appeared. It is undoubtedly from one or other of these related groups that the mammalian ancestor arose but it must not be supposed on that account that the first Mammals appeared in Africa. From the history of the Insectivora and other mammalian orders we learn that the early Mammals very probably evolved in the Northern hemisphere and that the less adaptable members of the class, as previously suggested, migrated southward when the climate in the north changed. Upon this hypothesis we should find in South Africa only the more specialized primitive members of the group. We do not look to any one of these South African forms as the actual mammalian ancestor but we know that in many features they must closely resemble it. Existing Fishes and Reptiles, none of which are at all close to the hypothetical line of mammalian descent, have already taught us certain lessons in the phylogenetic development of tooth forms. Thus it is with the South African fossils: none of them represents the actual mammalian ancestor but from them we can reconstruct stages in mammalian evolution with a fair degree of probable accuracy.

In the Therocephalians the first maxillary tooth became caniniform and with this change the temporal muscles increased considerably in size and strength. In its turn the growth of the temporal muscle brought about an enlargement of the temporal fossa and induced the appearance of the coronoid process in the mandible. A zygomatic arch of mammalian

type also appeared for the first time. In consequence of the development of the coronoid process and the greatly increased size of the dentary element in which the teeth are lodged the Therocephalian mandible began to assume a somewhat mammalian appearance.

The Cynodonts in general were much more mammal-like than the Therocephalians. They possessed a secondary palate, a large median unpaired vomer and two occipital condyles. The dentary increased so greatly that it constituted almost the entire mandible. The teeth differentiated into incisors, canines, premolars and molars. According to Broom it is probable that these mandibular and dental changes together with a narrowing and deepening of the snout resulted in the formation of the secondary palate. The method of articulation of the mandible with the skull even in Cynodonts is however still typically reptilian.

If then Dr. Broom's theory proves correct we may take it that in Triassic times the mammalian ancestors were either Cynodonts or Cynodont-like Therocephalians. One feature distinguishing these creatures from other more primitive Reptiles was the possession of well-developed limbs by which the animal was raised off the ground. Our common Horned Toad has limbs developed to the stage of supporting the body above the ground only in the act of walking. It can represent for us the early Reptile flattened dorso-ventrally, the limbs of which besides subserving the more primitive function of locomotion are becoming adapted also for the purpose of support. It has been suggested that the similar change of gait exhibited by the Therocephalians was due to development of the brain but it is altogether inconceivable that at so early a stage of animal history the brain could have such influence upon the body. It is more natural on the contrary to believe that conversely changes in the brain resulted from the altered mode of locomotion. The Cynodonts show a relatively great development of the cerebellum which seems to be accounted for by the increased coordination of movement entailed by the new walking habit

Therocephalian Ancestor

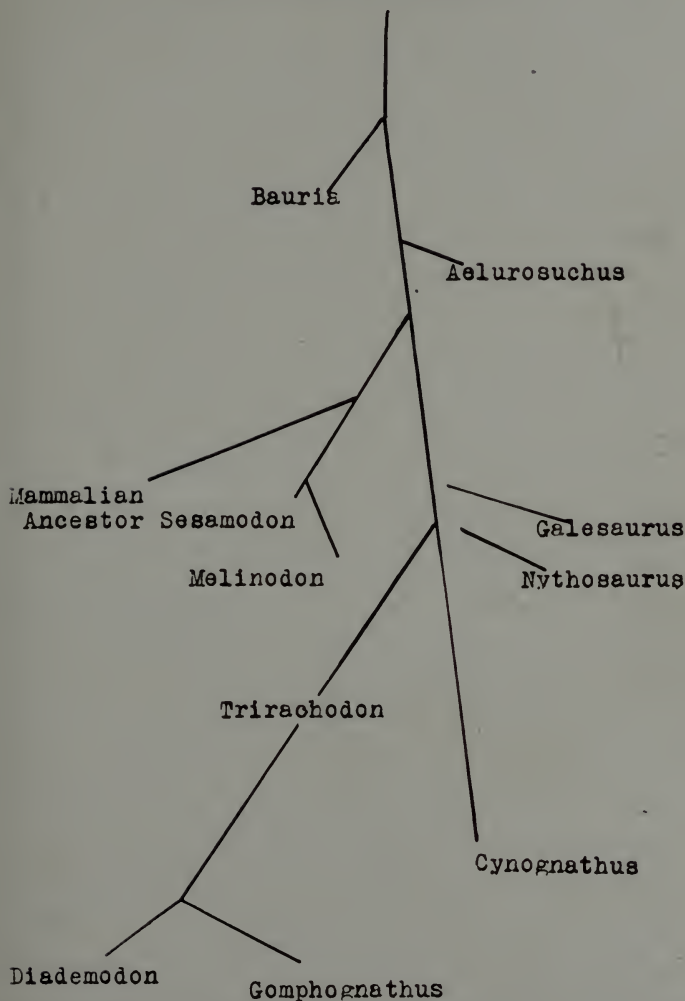


Fig. 9.—Genetic relationships of the principal known Cynodonts. (After Broom.)

and greater activity. It is Broom's interesting surmise that this greater activity ultimately brought about the development of the warm-blooded Mammals.

After this brief general outline it will be instructive to turn to some of the Cynodonts most nearly related to Mammals in order to observe the gradual appearance of mammalian traits.

The two South African Triassic Cynodonts *Bauria* and *Sesamodon* are probably nearest to the direct line of mammalian evolution. Although almost certainly a Cynodont *Bauria* retains many of the Therocephalian features and thus represents a comparatively early ancestral stage. In spite of the fact that it is less mammal-like than certain other Cynodonts *Bauria* exhibits some mammalian characters which the higher forms have lost. *Sesamodon* is interesting because it displays most of the mammalian characters of *Bauria* and in addition presents the majority of those found in other higher Cynodonts. The relations of the various mammal-like Reptiles, now to be discussed, to each other and to the hypothetical mammalian ancestor are diagrammatically shown in Broom's table (Fig. 9).

Examination of the restored skull of *Bauria* (Fig. 10) shows that the teeth fall into incisor, canine and premolar-molar series. The last mentioned are numerous, comparatively small, and simple in form; the canine as in Mammals is represented by the first maxillary tooth. The dentary element forms the greater part of the mandible which exhibits a well marked coronoid process but articulates with the skull in typical reptilian fashion by a joint between the articular element and the quadrate, the latter invisible in the illustration because of the laterally overlapping squamous. The skull no less than the mandible and teeth presents a general mammal-like appearance. The temporal fossa is large and incompletely separated from the orbit by a process of bone which though analogous is not homologous with the process separating the temporal fossa from the orbit in Mammals. In the Cynodont this process is formed by a special bone, the postorbital, which disappears in the Mammal and is replaced by the postorbital process of the frontal. The zygomatic arch is not powerful and no process arises from the zygomatic bone to meet the postorbital. Strikingly

unlike the mammalian condition is the separation of the nostrils from each other in *Bauria* not by cartilage only but by an upwardly directed process of the premaxilla such as occurs in Amphibians, Birds and many other Reptiles. Another element in the skull of the Cynodont not usually found in Mammals although occurring in certain forms which have retained

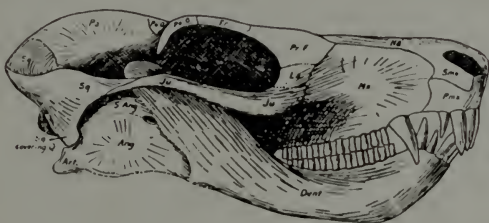


Fig. 10.—Side view of restored skull of *Bauria cynops*. (After Broom.) Abbreviations as in Fig. 8, A. Fr., frontal; Ju., zygoma; La., lacrimal; Mx., maxilla; Na., nasal; Pa., parietal; Pmx., premaxilla; PoO., postorbital; Smx., septomaxillary

very primitive features (*Ornithorhynchus*, *Echidna*, *Dasypus*) is the septomaxillary which in *Bauria* appears on the face between the nasal and the premaxilla but as we shall see later becomes partly submerged in *Sesamodon* and retires into the nose itself. In the undifferentiated condition of the pre-

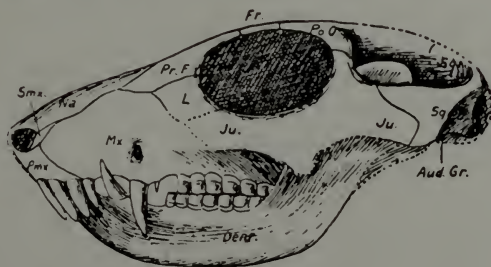


Fig. 11.—Side view of restored skull of *Sesamodon browni*. (After Broom.) Abbreviations as in Figs. 8-A and 10. Aud. Gr., groove for lodgment for external auditory canal.

molar-molar series, the absence of a complete postorbital arch, the large frontals and the condition of the septomaxillary *Bauria* approaches more closely than *Sesamodon* to the probable mammalian ancestor.

In *Sesamodon* (Fig. 11) as restored by Broom we see a Reptile in certain respects even more mammalian in appearance than *Bauria*. In this Cynodont the lower canine was long enough probably to overlap the maxilla when the jaws were closed; the first upper postcanine tooth is more conical than those succeeding it and illustrates the varying characters of the cheek teeth for which however we shall do better to con-



Fig. 12.—A. Palatal view of left maxilla of *Diademodon mastacus*. (After Seeley.) B. Lateral view of the left dentary of *Diademodon mastacus* with occlusal view of the seven lower molars of the right side. (After Broom.) Note the tubercular character of the crown, the elevation of the lateral cusps and the transverse elongation of the single roots of the maxillary teeth. In the mandibular molars note the smaller rounded crown and the single transverse ridge on the occlusal surface.

sult the illustration of *Diademodon*; the zygomatic is more powerfully built and sends a process upward; the mandibular articulation permits limited antero-posterior movement which is probably to be associated with the flat thick crowns of the

molars. In the occipital region of *Sesamodon* we note two condyles as in Mammals instead of the partially subdivided single median condyle reminiscent of Reptiles found in *Bauria*. The frontals like those of *Bauria* and unlike those of other Cynodonts enter into the formation of the orbits as they do in Mammals. Unlike the condition in *Bauria* the separation of orbit and temporal fossa is complete owing to the large size of the postorbital bone, an element non-existent in the Mammal.

Before leaving this important group it is necessary to refer to certain features illustrated by other and more specialized species. Very significant is the possibility in many Mammals of a lateral movement of the cheek teeth when the jaws are closed and the incisors locked. This primitive triturating movement is already foreshadowed in *Sesamodon* and in *Cynognathus* (see Fig. 9).

The number as well as the character of the teeth is important. *Aelurosuchus*, the cheek teeth of which are not known, possessed on each side five incisors and a canine in the upper jaw, four and a canine in the mandible; its dental formula can therefore be expressed:

$$I \frac{5}{4}, C \frac{1}{1}, P ?, M ?.$$

Diademodon, (Fig. 12) another Cynodont described by Seeley and Broom, possessed four premolars and seven molars; its formula therefore is:

$$I ?, C ?, P \frac{4}{4}, M \frac{7}{7}.$$

The lower premolars increase in size from before backward and the fourth projects more from the mandible than the first molar. Each displays two cusps, a larger outer and an inner. The molars are much bigger teeth than the premolars but nevertheless exhibit the reptilian character of a single root. Those of the upper jaw are larger; they are broader transversely, compressed antero-posteriorly and between them the lower molars occlude. Each of the mandibular molars, like the pre-

molars presents an outer and an inner cusp connected by a well developed slightly concave ridge dividing the crown into a posterior half which engages the corresponding maxillary tooth and an anterior half which occludes with the maxillary tooth next in front. The larger outer cusp fits between and internal to the corresponding cusps on the two upper teeth with which the lower molar occludes. In addition to the main cusps and ridge each molar presents a number of small cusps on both anterior and posterior margins. The crown of each maxillary molar exhibits two lateral cusps of which the anterior is the larger and three medial cusps decreasing in size from before backwards. Some smaller cusps lie along the posterior margin. From the prominent anterior lateral cusp a transverse ridge connecting with a cusp on the medial aspect divides the crown into two parts which occlude with the lower teeth as previously indicated. It is to be observed further that the elevation of the maxillary molar crown was probably greatest in the middle of the series so that from front to back of the jaw the molars, as in many mammalian forms, exhibited a convex curve.

Although at one time thought to be of herbivorous habit it is now believed that *Diademodon* was a carrion feeder: its dentition seems to indicate a degenerate carnivorous type. The temporal muscles must have been enlarged as in Carnivores and the molars though worn show no such great attrition as might be expected to result from a vegetable diet. But the crowns are flat-topped, the cusps not very well marked and the last molar smaller than the preceding tooth, all features indicating departure from the primitive type.

The features of the *Cynodont* dentition have been dwelt upon in some detail since they show so many striking analogies to the dentition of mammals and seem to illustrate a tendency shared in common with the Mammalia and other mammal-like creatures to develop along certain general lines. This inherent tendency on the part of teeth in phylogeny to respond in somewhat similar fashion to similar environmental conditions will frequently engage our attention in the succeeding parts of this

book. It may be wondered how teeth which seem so stable should have the power of change. The changes which we observe are not those between one generation and the next, but the accumulated modifications of many successive generations. As stated in the first chapter these changes are probably due to the occurrence of minute abrupt mutations linked in vast numbers and appearing adaptively in certain definite directions. We are as yet in the dark regarding the manner in which these modifying mutations are correlated or induced. They occur as if in response to mechanical requirements but though they resemble acquired characters they are transmissible.

THE PROTODONTA

Another group of animals occurring in Triassic times calls for some attention. We know but three members, all tiny creatures two of them from the upper Triassic of North Carolina. They have been classed as Mammals since the mandible of each apparently consists of a single bone. But we cannot absolutely eliminate the possibility that some elements entering into the formation of the mandible during life are unpreserved in the fossil remains.

The two North Carolina mandibles are represented in Fig 13; the upper is that of *Microconodon*: the lower *Dromatherium*. The latter shows differentiation of the teeth into incisors, canines, premolars and molars, and we may infer that this was true of the former also. In each case the molars are larger and display more cusps than the premolars. The jaws are unlike those of Mammals since the condyle and coronoid process with the intervening sigmoid notch are but poorly developed and in *Dromatherium* the incisors extend down on to the front of the symphysis. Further both mandibles differ from those of the Mammals of the next geological period, the Jurassic, in presenting a considerable diastema directly behind the canining yet the molar teeth unlike those of Reptiles show

a depression at the base of the crown indicating incipient division of the root into two.

Although these fragmentary specimens undoubtedly represent stages in the evolution of the Mammal they are probably too specialized to be actual mammalian ancestors. Having noted their mammal-like characters we can but say as we said of the Cynodonts that Mammals probably arose from some

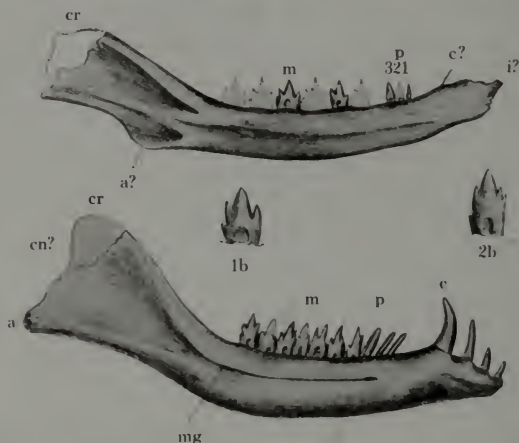


Fig. 13.—Mandibles of *Microconodon tenuirostris* (upper figure) and *Dromatherium sylvestre* (lower figure). (After Osborn.) The mandible of *Microconodon* is seen from the lateral and that of *Dromatherium* from the mesial aspect. Abbreviations.—a., angle; c., canine; cn., condyle; cr., corenoid; i., incisors; mg., groove for Meckel's cartilage; m., molars; p., premolars; 1b, the fourth or fifth molar of *Microconodon* and 2b, the second molar of *Dromatherium* both much enlarged.

creature like them: that Nature was trying her hand and these represent one of her many experiments which, since it did not ultimately succeed, was discarded after trial.

THE MULTITUBERCULATA

Another group of Mammals representing one of Nature's trial efforts is that known as the Multituberculates. These animals like the Protodonts first appeared in the Triassic but lingered on until the Basal Eocene when they finally became extinct. From certain skeletal features we infer that they were marsupial in character but in no direct way allied to modern Mar-

supials. The most distinctive trait of the Multituberculates is the many-cusped appearance of the molar teeth. Since these animals existed at a period so early in mammalian history and because of the fact that the probable ancestors of modern Mammals when first encountered* present molars with several cusps it has been suggested that the existing mammalian dentition may have been derived from that of a primitive ancestor with many-cusped molars. This hypothesis is known as the Primitive Polybuny Theory. Later investigation has shown that the Multituberculate dentition probably is either of independent origin or derived by reduction from the primitive Prototherian dentition, and although some modern Mammals recall this type in certain features, the features in question are in reality secondary results of convergent evolution. The Multituberculates therefore are no longer considered as the parent stem of modern mammalian forms.

THE JURASSIC MAMMALS

It is in the next geological period, the Lower Jurassic, that we find the first examples of mandibles which we can be sure are mammalian and they indicate immediately that we are once again observing Nature's experiments. The Jurassic Mammals clearly fall into two categories each quite distinguishable from the other, the Triconodonta and the Trituberculata. Of these as of so many other fossil animals the mandible is the bone by far most commonly found.

The Triconodonta

In the mandibles of certain Triconodonts illustrated in Fig. 14 can be observed a low lying sessile condyle recalling in its position the articulation of the Cynodonts, a broad coronoid process and an angle more or less inflected as in recent Marsupials. The teeth of Triconodon show three cones arranged in an antero-posterior line. Of these the middle one tends to be

*See section on Trituberculates.

the highest. In *Menacodon* the two smaller cones lie somewhat on the internal or lingual aspect of the larger middle one. *Spalacotherium* presents the two lesser cones adjoining at their bases on the inner aspect of the larger middle cusp, their tips being directed respectively forward and backward. In all

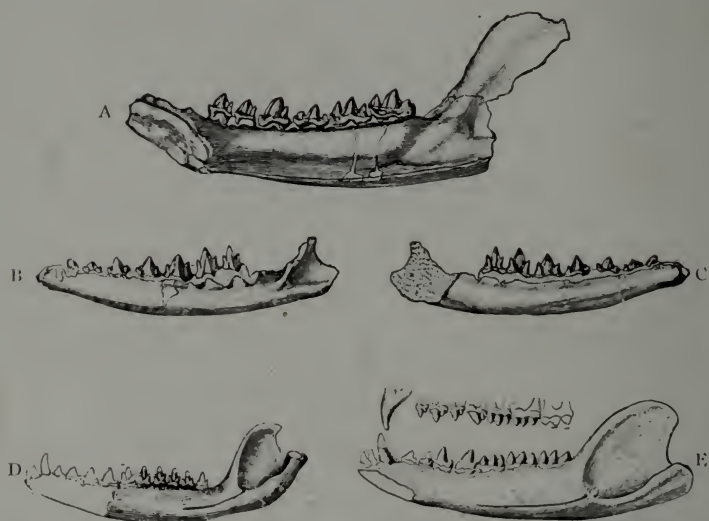


Fig. 14.—Jaws of Jurassic Triconodonts. (All after Osborn.—*Menacodon* and the upper figure of *Triconodon* originally after Marsh. Enlarged.)

- A. Mesial aspect, *Triconodon*, America.
- B. Mesial and C. lateral aspects, *Menacodon*, America.
- D. Mesial aspect, *Spalacotherium*, America.
- E. Mesial aspect, *Triconodon*, England.

these mandibles the molar teeth show a strong internal ridge or cingulum.

The most generalized of all the Triconodonts is *Amphilestes* with the dental formula:

$$I \overline{4}, C \overline{1}, P \overline{4}, M \overline{7}.$$

which is identical with that of the Cynodonts previously mentioned. The premolars in this group as in the Cynodonts steadily increase in size from before backward to culminate

in the last which projects more than the first molar. It should also be noted that in *Triconodon* the fourth postcanine tooth alone is replaced by a successor.

It was from *Triconodont* mandibles that Cope many years ago formulated his theory of a migration of the lesser cones from their original position to form ultimately a triangle with the larger cusps. This view is not held at the present day but in view of its historic importance as an early enunciation of the Theory of Trituberculy we shall recapitulate the two propositions in the original presentation of the theory by Cope and Osborn.

(1) In the more advanced *Triconodonts* the upper and lower molar crowns are shaped like reversed triangles shearing past each other. In the upper jaw the triangular three-cusped crown is called the *trigon*; in the mandible the *trigonid*. In essence the Tritubercular Theory calls for the derivation of modern mammalian molar teeth from similar reversed triangles and this part of the theory is still held to be correct. In the upper molar the large internal cusp forming the apex of the trigon is called the *protocone*. In the lower molar the outer cusp which at first was thought to be homologous with this since it also forms the apex of the triangle is the *protoconid*. The *paracone* and *metacone*, the former in front and the latter behind, lie at the basal angles of the upper molar triangle and the analogous *paraconid* and *metaconid* occupy corresponding positions on the lower molar crown. The suffix *id* was given to the cusps of the mandibular teeth to distinguish them from the supposedly homologous cusps of the upper teeth. It is now recognized however that the *protoconid* is the homologue of the *paracone* and not of the *protocone*.

(2) According to the original enunciation of the Tritubercular Theory the para- and metacones or -conids primitively lay in a straight line with the main cusp but later in phylogeny their positions relative to this cusp alter and thus the triangular crown was formed. It may possibly be that such a mode of evolution did occur in the molar teeth of the Jurassic Tri-

conodonts but it is no longer considered probable that such a cusp migration took place in any other group of Mammals recent or extinct.

The Trituberculata

The other group of Jurassic Mammals, known as the Trituberculates, differs quite extensively from the Triconodonts. *Amphitherium* which is represented by the mandible only is probably the most generalized species known. It appears to have possessed five premolars and six molars, each of these

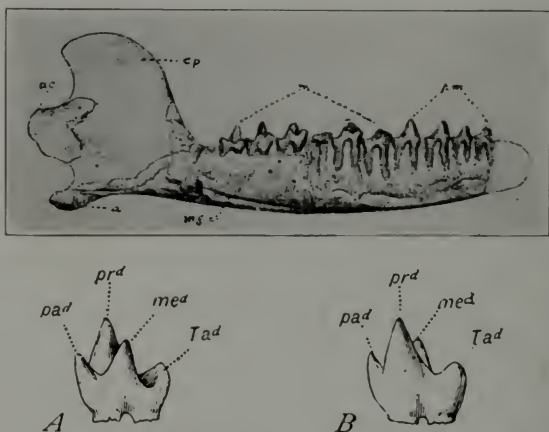


Fig. 15.—Lateral aspect, mandible of *Amphitherium prevostii*, Middle Jurassic, England. (After Goodrich, Enlarged.) Restored right mandibular molar of *Amphitherium prevostii*. (After Goodrich.) A, mesial aspect; B, lateral aspect; Abbreviations, a, angle; ac, condyle; cp, coronoid process; m., molars; me^d., metaconid; mg., groove for Meckel's cartilage; p., premolars; pa^d., paraconid; pr^d., protoconid; Ta^d., talonid. Note the bifanged character of the cheek teeth, a typically mammalian feature, the conical premolars and the primitive tuberculo-sectorial molars. The angle in this species is partly inflected.

postcanine teeth being provided with two roots. The total number of postcanine teeth is the same as in the Triconodonts and in the Cynodonts previously described. Since the teeth of the actual specimen are somewhat worn the enlarged restored models (Fig. 15) give a better idea of the molars of this animal. These differ greatly from the Triconodont molars. The large central protoconid is very prominent and, as in the

foregoing group, occupies the buccal aspect of the tooth. The paraconid unlike the condition in the Triconodont is not sub-equal with, but smaller than, the metaconid which lies internal rather than postero-internal to the protoconid. There is also a further structure, a kind of heel, developed on the posterior aspect of the tooth; this has received the name *talonid*. In *Amphitherium* there is but one cusp, the *entoconid*,* upon the heel. No cingulum is developed. The lower molars of *Amphitherium* differ very considerably from those of Triconodonts in the relationship in size between the paraconid and metaconid, in the position of the metaconid relative to the protoconid and in the absence of the internal cingulum. The mandible also of *Amphitherium* is built upon a plan slightly different from that of the Triconodont. The angle is not inflected in one species though it is in another and whereas the condyle seems to be sessile and the coronoid process broad in *Amphitherium* itself the related form, *Peramus*, shows a narrowing of the coronoid and a slight suggestion of a neck on the condyle.

In *Amphitherium* as in the Triconodonts there is a sharp differentiation between premolars and molars and the former teeth increase in size from before backward until the last is even more elevated than the first molar. In both respects these Jurassic Mammals resemble *Diademodon*. The tooth formula:

$$P \frac{-}{4}, M \frac{-}{7}.$$

is fairly characteristic of all these three types and may have been a primitive feature inherited by both Triconodonts and Trituberculates from a remote common ancestor but the marked differences between the teeth of the two Jurassic groups of Mammals indicate that they must have evolved on long separate and divergent lines.

We know the upper jaws of three examples of the Trituberculates and to these should probably be added a fourth. As

*Behind the metaconid. Later we shall find that two other cusps develop on the heel, the *hypoconid* behind the protoconid, and the *hypoconulid* axially and posteriorly.

a type molars of *Dryolestes* are figured (Fig. 16). The upper molars are dissimilar in form from the lower molars and in this the Trituberculates differ from the Triconodonts. The upper molars again are very wide transversely and larger than the lower molars. The protocone on the inner side of the crown fits like a pestle into the mortar-shaped talonid of the corresponding lower tooth. Paracone and metacone are present and between the latter and the protocone a smaller cusp, the *meta-*

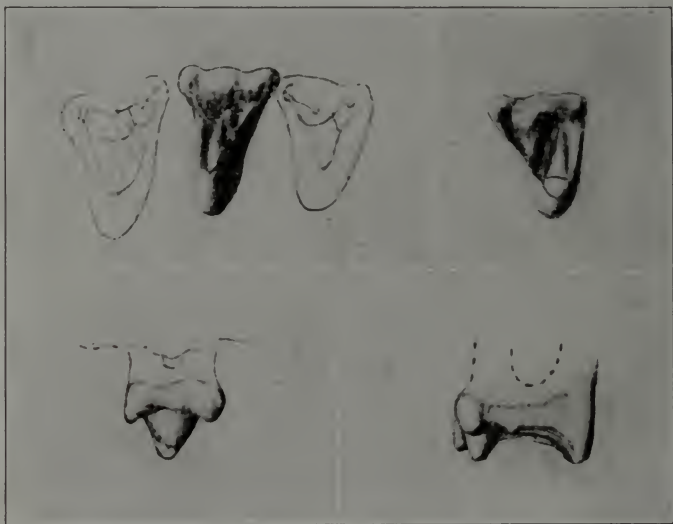


Fig. 16.—Molar teeth of *Dryolestes* sp. Jurassic, America. (After Gidley.) Upper figure. Left upper molars (left) and first right upper molar (right). Lower figure. Left upper molar, lateral (right) and posterior (left) views. *Dryolestes* represents a stage in which the upper molars, though more numerous (8) than in higher Mammals, were narrower antero-posteriorly.

conule. On the buccal side of the para- and metacones are two outlying cusps, the *parastyle* and *metastyle*.

In later Mammals we shall see that as the talonid grew larger and more prominent the protocone became depressed. A further cusp, the *hypocone*, began to appear from a spur-like internal cingulum and fitted into the trigonid of the lower molar next behind. The hypocone is the cusp of the *talon* or

heel of the upper molar. Whereas the talonid may have even three cusps the talon never possesses more than one. These facts are mentioned at this stage merely to indicate in what manner the upper molars increase in complexity. No hypocone is exhibited by the molars of Jurassic Mammals. If one examine the posteanine teeth of modern or even of Tertiary Mammals the striking similarity of the last premolar to the first molar suggests that the premolars represent stages in the development of the molars. This resemblance gave rise to the Premolar Analogy Theory the basic principle of which is that the premolars exhibit simpler stages in the formation of the molars. Premolars were distinctly marked off from molars even in Triassic times (*Diademodon*, *Protodonta*). The similarity which they exhibit to the molars in Tertiary and in recent Mammals has been explained on this account as an example of convergent evolution. But we have already noted that there has been no migration or rotation of cusps as was formerly thought to have occurred in the ancestral history of Mammals and, further, that the paracone of the upper molar and not the protocone is the real homologue of the protoconid of the lower tooth. There is therefore no reason for retaining the Scott-Osborn view that the outer cusp of the upper premolar is the homologue of the inner cusp (protocone) of the molar. Inasmuch as the premolars in many Mammals increase in complexity from before backward up to the fourth which resembles but is less complex and more primitive than the first molar, it now appears likely that as exemplified by some mammalian forms the premolars do represent stages in the history of the molars. In the Horse the premolars have taken on a completely molariform appearance; in the Dog they have shown little tendency to become molariform at all. These are not examples from which information can be gleaned regarding the relationship of premolar patterns to stages in molar formation. The dentition of the Tapir illustrates the case much better for in the premolar series of this animal each successive tooth is more molariform until the last is barely distin-

guishable from the first molar. In the main then the Premolar Analogy Theory as presented at the present day is correct.

The latest presentation of the Theory of Trituberculy as set forth by Gregory, while emphasizing the belief that the paracone actually represents the summit of the primitive reptilian crown and is therefore homologous with the protoconid, insists that the primitive condition of the molars in both jaws was one of reversed triangles or wedges, that the upper and lower molar crowns were not alike but strikingly dissimilar and that there has been no migration of the cusps which originally appeared in the situation where they now exist. According to this "Wedge" Theory the ancestors of the Trituberculates were neither Triconodonts nor Protodonts but some unknown Cynodont with transversely widened upper molars. In Trituberculates the upper molars may indeed be called tritubercular whereas the lower teeth have always possessed a heel or talonid in addition to the trigonid and are therefore more properly termed tuberculo-sectorial teeth. We shall follow these same types in the differentiation of the teeth of modern Mammals and we shall note that of the two the lower molar is the more stable in pattern.

Recent search among fossil animals for a parent type of later Mammals has established the claim that modern Mammals originated from Jurassic Trituberculate-like forms but the ancestry of the Trituberculates themselves is obscure.

In computing the relative age of marsupial and placental Mammals it is interesting to speculate upon the precise relationship of the Trituberculata. Trituberculates like *Amphitherium*, as indeed Triconodonts also, exhibit many characters now best illustrated by the Marsupials. But many of these features may be and probably are specializations and indicate merely that the animals are not directly in the mammalian ancestral line. The same features may be found in the more specialized Placentals. Varying inflection of the mandibular angle for example is exhibited in slight degree by several

modern placental Mammals. For the present therefore it is probably safest to consider that the Trituberculata represent a class of animals from which both Marsupials and Placentals have arisen.

CHAPTER IV

THE RELATION BETWEEN LIFE HABITS AND DENTITION

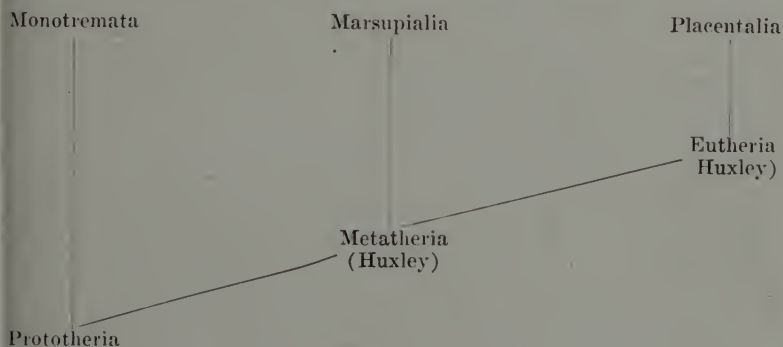
THE MARSUPIALS

Distinctive features of mammalian subclasses—Origin of Marsupials—Characters of primitive and of marsupial skulls—Plexodont Theory—Description of marsupial dentition—Aberrant forms—Reasonableness of the persistence of the tritubercular tuberculo-sectorial dentition—The marsupial milk dentition—Reversion, divergence and parallelism in evolution—Species formation.

In the last chapter the origin of modern Mammalia has been considered and the Jurassic Trituberculates have been indicated as exhibiting most clearly the features which probably characterized the ancestor of the Mammals of today. Instead of following the theme in Paleontology it is now proposed to discuss existing Mammals and to show by these whenever possible the adaptation of teeth in response to animal habits and environment.

We have used the terms *marsupial* and *placental* on several occasions and it now becomes imperative that these terms should be clearly defined. Existing Mammals are divided into egg-laying (oviparous) and non-egg-laying (viviparous) subclasses. The modern representatives of the former, the Duck-bill and the Spiny Anteater, we shall discuss in due course and shall find that they are survivals of a very early primitive type of Mammal. Such primitive Mammals, among which must be referred the Protodonta already described, are known as Prototheria. The higher subclass comprising the viviparous

Mammals received from Gill the name Eutheria. This term unfortunately was used in a more restricted sense by Huxley to signify merely the Placentals and their immediate ancestors. The Marsupials and their ancestors (from which also the hypothetical placental ancestors arose) Huxley considered a subclass in themselves and termed the group the Metatheria. This subclass is now considered an infraclass of the subclass Theria (Parker and Haswell) the other infraclass being the Eutheria (Huxley). The relations of these various groups are presented in diagrammatic form below, the terms being used in the significance which Huxley gave them to signify successive stages of evolutionary development (after Bensley).



A placental Mammal differs from a Marsupial in its more advanced type of placentation and in remaining in the uterus until it has attained a higher degree of development. From the chorion of the fetus in the placental Mammal villi penetrate into the maternal mucosa to form a "placenta." No placenta is formed in the case of the Marsupial* and the young are born in a very immature state. After birth they are placed by the mother in the marsupium or pouch† where they attach

*The Marsupials differ quite considerably in the form of their placentation, the Bandicoot (*Perameles*) and the Dasyure (*Dasyurus*) presenting a type most nearly like that of true Placentals.

†The pouch is present in most but not in all Marsupials.

themselves to the maternal teats, remaining thus until capable of looking after themselves until which time they are nourished by injections of milk induced by periodic contractions of the breast musculature. The pouch is really a mere fold of abdominal skin and is temporarily or permanently present according to the species. The Marsupial represents a very ancient type of Mammal probably older than the Placental.

In addition to the distinguishing characters relative to birth and the genital organs Marsupials present other features some of which we may note as differentiating them from placental Mammals. Of these the inflection or inbending of the mandibular angle is a character present in all but one of the Marsupials although occurring to a less extent in the Insectivores and in a few Rodents. The condyle is low and sessile and the sigmoid notch shallow. The brain case is relatively narrow and in consequence the zygomatic arches project very obviously. The sutures tend to remain open long after the animal reaches adult life. The nasal bones increase in breadth backward. The malar or zygomatic forms part of the glenoid fossa. The tympanic remains throughout life a simple ring unfused with surrounding bones. The great wing of the sphenoid forms part of the tympanic bulla. Fenestræ or openings occur in the hinder part of the palate. Not all the foregoing features are truly primitive but taken together they clearly distinguish the skull of a Marsupial from that of a placental Mammal.

In the Marsupial there may be as many as five incisor teeth in each side of the upper jaw whereas in a placental Mammal there are rarely more than three. The incisor teeth in the Marsupial usually differ in number in upper and lower jaws. The premolars are never more than three in number, the molars usually four and sometimes more.* In Placentals four premolars and three molars represent the maximum.† A fur-

*In order to bring the Marsupials into harmony with placental Mammals some writers describe the first molar as a premolar, thus attributing to the Marsupial four premolars and three (or more) molars. The older usage is followed in this volume.

†Except in a few Placentals, for example the Large-eared Wolf of South Africa (*Otocyon*) which has four lower molars on each side. In some Armadillos and in some Cetacea the postcanine teeth are increased in number.

ther feature of the dentition in the Marsupial is the fact not clearly explicable at present that only one tooth at most namely the last tooth preceding the molars possesses a successor. This condition also occurs in the Jurassic Triconodon.

It is probable that the reduction of the milk dentition in Marsupials is a secondary specialization like the pouch formation and associated peculiarities relating to birth. The Miocene *Santa Cruz* formation of Patagonia has yielded the skeletons of certain undoubted Marsupials which show no fenestration of the palate. In these animals the milk dentition is not so greatly reduced as in modern Marsupials nor incidentally as in the Jurassic Triconodon: the canines and one or two post-canine teeth (milk molars) possess successors. The enamel of the teeth also in the only form in which it has been microscopically examined resembles the enamel of placental Mammals. It may therefore be inferred that in diverging from their ancestral prototypes modern Marsupials have specialized in many features.

Among the existing Marsupialia are forms almost as minute as the smallest Placental, others large like the Kangaroo and powerful like the Tasmanian Wolf. Inhabiting only Australasia and the Americas, represented indeed but sparsely in the latter continent, they comprise the last remnant of a host which once inhabited the entire northern hemisphere.

The Marsupialia comprise arboreal, terrestrial and fossorial animals. Some of the terrestrial forms run, others leap, a few are semiaquatic. In respect of diet there are insectivorous, omnivorous, carnivorous and herbivorous species. Yet with all this variation in life habits the Marsupials belong to a single mammalian order; all are relatively closely akin. Hence they form a group in which may be traced better than in any other the structural modifications of teeth associated with change of habit. Marsupials as an infraclass are very ancient and the precise relationships in ancestral history of the suborders existing today are not very clear. They are probably all derived

from some generalized Polyprotodont form of the Upper Jurassic.

The most primitive Mammals were probably small insectivorous or insectivorous-omnivorous forms with teeth resembling those of the Trituberculates and of slow-moving terrestrial or arboreal habit. It may be advantageous at this point to enumerate certain features characteristic of the primitive Mammal and at the same time to state the relationship of these primitive features to the marsupial skull. By comparing the following tables it will be clear that, although modern Marsupialia display a greater number of primitive features and may be assigned a longer ancestry than placental Mammals, yet in certain respects the latter present more primitive traits.

Primitive Characters

FOUND INDIFFERENTLY IN MARSUPIALS AND PLACENTALS

SIZE:	Small.
TEETH:	Adjusted for insectivorous omnivorous diet. Incisor rows parallel or obliquely inclined to each other. Canines large. Premolars increase in size backwards. Molars increase in size backwards. Milk dentition well represented.
MANDIBLE:	Condyle sessile; at or about the level of the teeth. Coronoid broad. Sigmoid notch shallow. Angle inflected.
SKULL:	Brain case very narrow. Zygomata projecting. Sutures open. Nasals broader behind. Lachrymal extends on to face.

Features Differentiating Infraclasses of Theria*

	<i>Metatheria (Marsupials)</i>	<i>Eutheria (Placentals)</i>
TEETH:	Upper incisors often more than 3. Premolars never more than 3. Molars usually 4.	Upper incisors never more than 3 (except shrews). Premolars may be 4. Molars rarely more than 3, (Cetacea, Armadillos, Otocyon).

*It is not to be supposed that each of these characteristic features is to be found in every example of marsupial or of placental Mammals.

	Only one successional tooth at most (last premolar).	Milk dentition usually well represented.
	Different teeth modified for sectorial purposes.	P4 M1 modified as sectorial or carnassial teeth.
MANDIBLE:	Condyle sessile. Sigmoid notch shallow. Angle inflected.	Condyle with neck. Sigmoid notch deep. Angle rarely or but slightly inflected.
SKULL:	Brain case very narrow. Zygomata projecting greatly. Sutures remain open late. Nasals broader behind. Malar reaches glenoid fossa. Palate fenestrated.	Brain case broader. Zygomata projecting less. Sutures close earlier. Nasals broader anteriorly. Malar does not reach glenoid fossa. Palate not fenestrated.

Before passing to the actual description of marsupial dentitions, it is opportune to refer to an interpretation of tooth evolution which has not yet been mentioned, namely that developed by the late Dr. Ameghino and known as the Plexodont or Progressive Simplification Theory. The oldest Mammal known which approximates the modern type, *Proteodidelphys*, from the Cretaceous of South America presents, as would be expected from its Trituberculate ancestry, a tuberculo-sectorial type of molar. We have already noted that this type of molar when first encountered is fairly fully developed and nothing is known of how it evolved.

According to Ameghino it is probable that the molar type developed rapidly and to do this must have resulted from the fusion of a number of teeth each presenting a simple conical crown and a single root. Furthermore according to this theory, as in the Polybunary Theory previously discussed, all simpler forms of teeth found among Mammals today have resulted from progressive simplification. A little reflection upon the features of the reptilian and early mammalian teeth presented in the foregoing pages will convince the reader that the basal assumptions of this theory are not warranted. It may therefore be dismissed as untenable.

We shall now proceed to the consideration of the dentition of the Marsupialia as a study in the adaptation of tooth forms to life habits. As a standard a fairly primitive type of animal must be taken. It must fulfill at least many of the requirements already laid down: thus it will be of small size, of insectivorous (or insectivorous-omnivorous) diet and of terrestrial or arboreal habit.

An animal fulfilling the foregoing requirements is the tiny



Fig. 17.—Occlusal view of dentition in Marsupial Mouse (*Phascogale flavipes*, 9.211-2). Compare the upper molars with those of *Dryolestes* (Fig. 16) and the lower molars with those of *Amphitherium* (Fig. 15). The scale in this as in all succeeding illustrations indicates millimeters.

Australian Marsupial Mouse (*Phascogale flavipes*). A glance at the photograph (Fig. 17) shows the marsupial character in the fenestrated palate, the inflected mandibular angle and participation of the malar bone in the glenoid fossa. The tooth formula is:

$$I \frac{4}{3}, C \frac{1}{1}, P \frac{3}{3}, M \frac{4}{4}, \text{total } 46.$$

The incisor rows approaching each other obliquely, the well

marked canines, the triangular transversely elongated upper molars and the typical tuberculo-sectorial lower molars indicate its primitive character. The characters of the molars recall at once the appearance of Jurassic Trituberculates. The sharp needle-pointed cusps and the presence of pronounced styles upon the upper molars (Fig. 18) proclaim its insectivorous diet. Nevertheless there are certain features which suggest that even in this animal some specialization occurs. The incisors on each side of each jaw are one less in number than in the American Opossums which in this respect are still more primitive. Again the third lower premolar is smaller than the second indicating that the former tooth is undergoing reduc-



Fig. 18.—Lateral aspect of skull of Marsupial Mouse (*Phascologale flavipes*, 9.211-2). Note the typical needle-like insectivorous cusps and the forceps-grip between the procumbent lower incisors and the median upper incisors. Very plainly shown are the two-rooted condition of the upper premolars and the deep groove analogous to subdivision on the upper canine root (see p. 3).

tion. In the main however *Phascologale* may be said fairly to represent a very primitive type of Marsupial.

Reference to Fig. 18 shows that all the lower incisors are procumbent and form a forceps-like occlusion with the similarly procumbent upper median incisors, a trait characteristic of the insectivorous dentition. The upper median incisors have their tips approximated though their bases are set widely apart.

Regarding the molars it should be remembered that the protocone of the upper tooth fits into the talonid of the correspond-

ing lower as a pestle in a mortar. Again the trigonid of the lower tooth shears behind the trigon of the upper next in front. Hence the protoconid and paraconid of the lower molar correspond to one blade of the shears while the metacone and metastyle of the upper form the other blade. It is especially important to emphasize this as a preliminary to the discussion later of carnivorous adaptations in teeth. Equally important is it to remember in connection with omnivorous and herbivorous modification that the first indication of triturating action is the mortar and pestle relation of the talonid with the protocone. Once these fundamental relationships of the upper and lower molars to each other are fully understood the reason for the imperfect development of the last member of both series becomes obvious. Having no lower molar to shear behind it the last upper has developed no metacone or metastyle. Also the last upper tooth being reduced and possessing an imperfect protocone the talonid of the last lower molar is incompletely formed.

The carnivorous adaptation of teeth is next introduced, first because it is simpler and more direct in its evolution than the herbivorous modification and secondly because there is a direct succession toward this adaptation in the family Dasyuridae to which *Phascogale* belongs.

Sarcophilus ursinus, the Tasmanian Devil, a purely carnivorous, powerfully built and very ferocious animal inhabiting Tasmania alone, is becoming rapidly exterminated by the farmers as the penalty of its depredations on the stock. This ugly and nocturnal animal, illustrated in Fig. 19, kills every creature which falls in its way and is not too large to attack: even sheep are not infrequently victims of its bloodthirstiness. The size of the skull is shown by the millimeter scale. The animal is about as large as a terrier though much thicker set and with shorter limbs.

The tooth formula is:

$$I \frac{4}{3}, C \frac{1}{1}, P \frac{2}{2}, M \frac{4}{4}, \text{total } 42.$$

The mandible as in all purely carnivorous animals retains the condyle on the level of the molar teeth. The corônoid is elongated and in consequence becomes less broad. The jaws are greatly foreshortened, packing all the teeth closely together and reducing the antero-posterior extent of the incisor portion. The shortening of the jaws is associated with the elimination of the last premolar, a process already foreshadowed by its reduction in size in *Phascologale*. Such shortening is not necessarily characteristic of a carnivorous dentition; it occurs only



Fig. 19.—Dentition of Tasmanian Devil (*Sarcophilus ursinus*, 9.211-5). An example of the short-jawed Carnivore with reduction of the premolar series. Compare the obliquity of the upper molar shear with that in Fig. 17.

in certain genera. The milk molar preceding the third premolar in most Marsupials, like its successor, does not occur in *Sarcophilus*.

Turning attention to the incisors, it is observed that these are small and more or less identical with each other except the upper median teeth which as in *Phascologale* retain the separated bases and approximated tips.* The incisor rows however

*This feature is better marked in some specimens than in others. It is not very clearly exhibited in the skull figured.

are almost transverse since these teeth are no longer required as forceps but form rasps for cleaning flesh from bones.

The canines are powerfully developed as is natural in a carnivorous type.

In the molars the development of shearing action is pronounced and all tritulating function is practically eliminated. In conformity with the adaptation of the molars to a pure shearing function the following modifications have occurred. In the upper teeth the protocone and paracone are reduced and the two anterior styles are nonexistent. On the other hand the metacone and metastyle are greatly developed. With the reduction of the protocone the hinder margin of the tooth swings round to bring the shearing edge more in line with the direction of the dental arch. This will be apparent if a ruler is applied on the figure to touch the metastyle and metacone of the third upper molar. The straight edge will pass across the second premolar of the opposite side. If the same test is applied to the third upper molar of *Phascologale*, the straight edge will pass through the second molar of the opposite side. In the lower molars the protoconid and paraconid are strongly developed and together form a shearing edge. The metacone is nonexistent though it is represented on the last tooth by a small cingular cusp. In all the talonid is greatly reduced, being represented by a small entoconid and an obviously decadent hypoconid. The last upper molar having no shearing function is very degenerate and since there is practically no protocone on this tooth the talonid of the last lower molar is also vestigial.

Another type of carnivorous adaptation, this time retaining the long jaw, is represented by *Thylacinus cynocephalus*, the Tasmanian Wolf (Fig. 20). The most striking feature of this animal which is larger than and almost equally ferocious with *Sarcophilus* is the fact that the jaws instead of being fore-shortened are lengthened, especially in the premolar region. This elongation has not interfered with the typical carnivorous arrangement of the incisors but has resulted in the re-

tention of the third premolar which since it is the largest of the premolar series represents an even more primitive condition than that of *Phascologale*. On the other hand the milk



Fig. 20.—Dentition of Tasmanian Wolf (*Thylacinus cynocephalus*, 9,211-4). An example of the long-jawed Carnivore. Compare the molar shear with those of Figs. 17 and 19. Note the excavation immediately in front of the canine on the upper jaw for reception of the elongated lower canine.

molar which is replaced by this tooth is small, functionless and shed very early.

The dental formula is:

$$I \frac{4}{3}, C \frac{1}{1}, P \frac{3}{3}, M \frac{4}{4}, \text{total } 46.$$

The incisors are arranged in almost transverse rows, the typical carnivorous rasping position. All the upper teeth are incurved and the median incisors do not show the separation of bases and the approximation of tips found in *Sarcophilus*.

The canines present the usual carnivorous size and strength.

The molars are modified for shearing action as in *Sar-*

cophilus but their general plan is not quite the same nor is the talonid so extensively reduced. The metacone and meta-style in the upper teeth and the protoconid and paraconid of the lower exhibit the typical carnivorous exaggeration and the posterior border of the upper teeth is swung round as in *Sarcophilus*. The metaconid in the lower molars is nonexistent. As can be seen from the retention of protocone and talonid in un-reduced form the last molar in both upper and lower jaws is more developed than in *Sarcophilus*. Indeed in the mandible the third molar presents the primitive character of being the largest of the series and has the best developed talonid into which fits the comparatively large protocone of the last upper molar.

The lengthening of the jaws, the presence and large size of the third premolar and the characters of the molars just mentioned indicate at once that *Thylacinus* is no near relative of *Sarcophilus*. Rather these two animals present in common a carnivorous adaptation of the teeth but they have attained some similarity in tooth form by quite dissimilar stages. (Even their ancestors are only distantly related.) *Sarcophilus* is a modified *Dasyure* and *Phascologale* represents a primitive stage in its evolution. *Thylacinus* had with *Phascologale* a remote common ancestor but that is the extent of the relationship.

So far in tooth adaptation the emphasis has been placed upon the shearing action of the trigon and trigonid. Next must be considered the development of the grinding or triturating action of the heel or talonid of the lower molar in conjunction with the protocone of the upper. An example of specialized omnivorous dentition is to be seen in *Thalacomys minor*, a Rabbit Bandicoot (Fig. 21). The present specimen is from South Australia. Its food consists of insects and worms together with roots, bulbs, berries, fallen fruits and other vegetable substances. In pursuit of these it must often dig and this fact has given rise to the mistaken idea that the animal lives in a burrow. It is about as large as a small rabbit,

has long ears and silky fur but a long tail with a crest of hair on the dorsal surface. The tooth formula is:

$$I \frac{5}{3}, C \frac{1}{1}, P \frac{3}{3}, M \frac{4}{4}, \text{total } 48.$$

The jaws are elongated and associated with this feature is the retention of the primitively large third premolar.

The upper incisors, five in number on each side, also represent a stage as primitive as that of the American Opossum. Although they and the lower incisors retain the insectivorous



Fig. 21.—Dentition of Rabbit Bandicoot (*Thalacomys minor*, 9,213-1). This is a very specialized form of omnivorous dentition. It is also one of the extremely rare instances where a cusp (the metacone) has apparently migrated. The elongation of the body of the third lower molar (one form of hypsodonty) is very clearly shown.

arrangement and the latter are also somewhat procumbent the crowns are flattened laterally and increase in antero-posterior length.

The canines present the great length usual in primitive Mammals.

The molars are quadrituberculate teeth adapted for grinding rather than for shearing insects or flesh. Unfortunately the dentition is somewhat worn in the specimen figured and some cusps are not so clear as could be wished. By tracing their

history through less specialized members of the family the method by which the molars have attained their present form is clearly demonstrated. In the upper teeth the protocone remains large, the paracone is small and what at first appears to be this cusp is really part of the parastyle (style b. Bensley). A remarkable and almost unique feature is the migration of the metacone toward the palate so that this cusp comes to lie immediately behind the protocone except in the last molar in which it retains its normal position. The fourth large cusp, occupying what is normally the situation of the metacone upon the crown, is really the mesostyle (style c. Bensley). Unlike the condition found in the carnivorous dentitions just described the metastyle is eliminated and the metacone has taken on a pestle action somewhat similar to that of the protocone. This peculiar conduct of the metacone is the single known instance of migration of a cusp in the teeth of modern Mammals and as such it is worthy of note. Only in one order (Amblypoda) is a similar condition found even among Tertiary Mammals. Migration of cusps in animals of Trituberculate origin is therefore of the rarest occurrence and this is significant in relation to Gregory's presentation of the Wedge Theory (See page 62).

In the lower molars there are two striking features, great increase in size of the talonid and the reduction of the trigonid. The former is clearly a grinding adaptation, the latter the natural result of an increasingly herbivorous diet. In the talonid which is raised as high as the trigonid there are two cusps, the entoconid and hypoconid except in the last tooth. The talonid fits itself as a mortar for the pestle-like action of the protocone. In the trigonid, although the paraconid is lost, there still exists a part of the shearing ledge running from the site where this cusp once lay to the protoconid: this with the two remaining cusps of the trigonid bounds a second mortar-like area against which occludes the metacone of the upper tooth next in front.

Yet another point should be observed in the molars of *Thalacomys*. The grinding of roots and other vegetable substances

which are of necessity mixed with earth must entail greater wearing of the molars than the purely insectivorous or carnivorous habit. In *Thalacomys* this has been provided for by the marked elongation of the body of the tooth, one variety of a condition known as hypsodonty. In other animals the term hypsodonty is used to indicate marked elongation of the cusps themselves.

A much more general form of omnivorous dentition is that presented by *Petaurus breviceps* the Lesser Flying Squirrel



Fig. 22.—Dentition of Lesser Marsupial Flying Squirrel. (*Petaurus breviceps*, 9,222-3). Example of an omnivorous dentition forecasting in many features the evolution of the herbivorous adaptation. Note the elongated lower median incisors and the quadrilateral crowns of the molars with their four rounded cusps.

(Fig. 22). It is true that the parachute flight of this animal indicates a certain specialization but its dentition is stated to be the same as that of its nonvolant parent form *Gymnobelid-eus*. Naturally, in spite of its name this creature is not a squirrel at all but a phalanger. It has a dentition most important in the present connection because it foreshadows the method of evolution of the truly herbivorous adaptation.

Petaurus is an arboreal animal, its structure rendering it ill adapted for terrestrial habits. Its diet consists partly of insects and partly of the blossoms of the *Eucalyptus* tree.

The tooth formula is usually given as:

$$I \frac{3}{2}, C \frac{1}{0}, P \frac{3}{3}, M \frac{4}{4}, \text{total } 40.$$

although the identification of the vestigial lower antemolar teeth is difficult. Many evidences of considerable specialization are present. The elongated lower median incisor, the reduced upper canines, the irregularity of the upper premolars, the vestigial character of the lower teeth between the median incisors and the molars, the reduction in size from before backwards of the molars themselves especially evinced in those of the upper jaw, and the inturning of the hinder ends of the upper dental arch all indicate specialization. There are however certain primitive features which cannot be hidden. For example the upper incisor tooth rows are directed toward each other in typical insectivorous fashion. The median incisors also are somewhat procumbent and have their tips approximated more than their bases. The third upper premolar shows no sign of reduction. The median lower incisors are procumbent and although elongated and greatly enlarged meet the uppers in true forceps manner. Beyond these features the dentition displays new traits for examination. The large size of the median lower incisors has resulted in foreshortening of the mandible and reduction or elimination of all the lower intermediate teeth. The molars themselves no longer present needle-like cusps or, in the case of the uppers, well marked styles so characteristic of the insectivorous dentition. Their cusps are rounded, mound-like or bunodont. The styles are practically nonexistent and all trace of shearing action is lost. In the upper teeth, in addition to the original proto-, para- and metacones a fourth cusp appears behind the protocone and is fairly well marked in all except the last tooth. This new cusp is called the hypocone and its importance as a second pestle

accessory to the protocone becomes evident. There is a slight ridge connecting the proto- and hypocones and indications are present also of ridges passing transversely from the proto- and hypocones to the para- and metacones respectively. Finally from the hypocone a ridge ill-marked as yet passes round the anterior margin of the tooth in front of the paracone and a similar crest originating in the hypocone runs round the posterior margin behind the metacone. All these features are deeply significant as forecasting the commencing herbivorous adaptation.

In the mandible the molars, excepting the first, are quadrilateral in shape and display four bunodont cusps, the protoconid, metaconid, entoconid and hypoconid. The paraconid is eliminated. There is a slight external ridge connecting the proto- and hypoconids. In the first molar not only is the paraconid absent but the metaconid is vestigial and the protoconid shows an appearance reminiscent of its relatively great development in insectivorous forms since it exhibits to a slight degree a sectorial character. These bunodont molars are very serviceable in triturating food for the pestle and mortar relationship of the protocone and talonid is aided by a similar interaction of the hypocone with the anterior slope in front of the protoconid and metaconid of the lower molar next behind.

All the Marsupials hitherto described have belonged to the suborder Polyprotodonta, so-called because they possess more than one functional incisor on each side of the mandible. *Petaurus* is the first example of the suborder Diprotodonta, the members of which possess only a single pair of functional incisors in the lower jaw. Referring then once again to the dentition of *Petaurus* it is seen that the second and third upper incisors merely act as stops to the long lower incisors. It will shortly be apparent that the dentition of the herbivorous Diprotodonts is developed directly from the insectivorous type through the omnivorous adaptation by a peculiar elongation of the median lower incisor. There is however no direct line of evolution in which all the steps may be followed. Hence it

is necessary to examine the dentitions of two animals which represent side lines in evolution.

Trichosurus vulpecula, the true Phalanger (Fig. 23), one of the so-called Australian Opossums, is an animal about the size and form of a small fox. It is common everywhere in forested

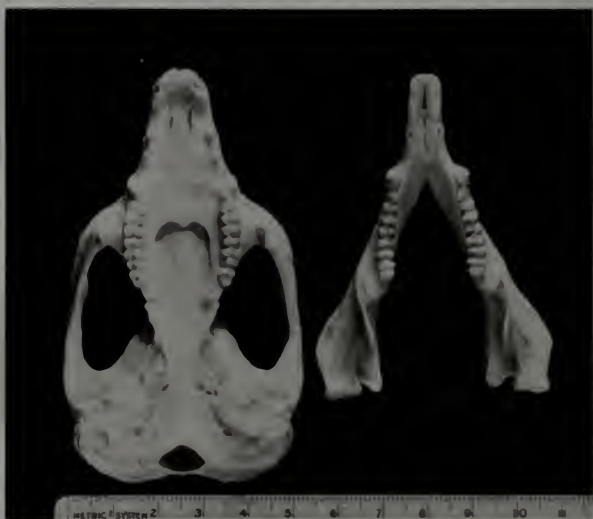


Fig. 23.—Dentition of the true Phalanger (*Trichosurus vulpecula*, 9.222-4). This dentition indicates still more clearly than that of *Petaurus* the evolution of the pure herbivorous type.

regions of the continent and its diet consists of small birds and leaves especially of the peppermint gum tree. The tooth formula is:

$$I \frac{3}{2}, C \frac{1}{0}, P \frac{2}{1}, M \frac{4}{4}, \text{total } 38.$$

The upper incisors are arranged in a somewhat carnivorous rasping arch and the last premolar of both jaws is sectorial in type, a form equally serviceable for cutting flesh or shoots. The canines are greatly reduced and the molars bunodont and roughly quadrilateral. The median lower incisors are elongated as in the herbivorous Kangaroos and the next incisors

merely vestigial. All other intermediate lower teeth in advance of the last premolar are eliminated. The upper molars show protocone, paracone, metacone and hypocone and from the first and last mentioned cusps which are connected by a low ridge there run ledges round the anterior and posterior margins of the tooth as in *Petaurus* but more strongly marked. All trace of styles has vanished. The hypocone is not developed on the last molar. Transverse ridges are well marked between protocone and paracone and between hypocone and metacone. Of the mandibular molars the first still shows some sectorial traits because of the relative prominence of the protoconid and the vestigial character of the metaconid. In the others the loss of the paraconid is obvious, although a remnant of the protoconid-paraconid ledge remains to form a triturating surface upon which the hypocone of the upper tooth next in front may play. The heel exhibits two well-marked cusps, the entoconid and the hypoconid, the latter of which is connected with the protoconid by a slight ridge. From the hypoconid a small ledge runs round the posterior border of the crown.

Before passing on to the lophodont Kangaroos we must note a type of purely herbivorous dentition with crescent cusped molars presented in the so-called crescent-toothed Phalangers. Of these the most advanced species is *Phascogalea cinereus*, the Koala or Native Bear (Fig. 24). This heavily built animal of the size and somewhat of the appearance of a poodle dog is never seen in captivity outside Australia because of the impossibility of obtaining the proper food. The animal lives largely upon leaves of the blue gum tree though it also descends to the ground at night to dig for roots. Its diet is thus purely herbivorous. The tooth formula is:

$$I \frac{3}{1}, C \frac{1}{0}, P \frac{1}{1}, M \frac{4}{4}, \text{total } 30.$$

The dentition is at once distinguished from that of the Phalanger by the absence of the rudimentary lower second incisors, the elimination of more antemolar teeth, the retention of styles

on the upper and the occurrence of crescent-shaped cusps on the lower molars. A feature of the mandible becoming more marked with an increasingly herbivorous habit is the raising of the condyle above the molar level with consequent increase in the area of the ramus, reduction in breadth of the coronoid process and clearer definition of the sigmoid notch. It is also worthy of note that in the more purely herbivorous forms the zygomata do not project so greatly beyond the brain case as



Fig. 24. Dentition of the Koala (*Phascolarctos cinereus*, 9,222-2). This is an example of the crescent-cusped molar pattern of the purely herbivorous dentition. The third upper molar is an example of reversed evolution.

in insectivorous and carnivorous forms. The upper incisors are no longer arranged as for rasping but obviously as a counter-cutting edge for the elongated and procumbent lower incisors. In this function the median upper teeth alone are important, the second and third incisors being greatly reduced. The upper canines are quite rudimentary; the lowers eliminated. The single premolar in each jaw still shows some remnant of a sectorial character. The molars, more especially those of the upper jaw decrease in size from before backward. One of the

most significant features is the occurrence of crescentic or selenodont cusps. In the upper teeth proto-, para-, meta- and hypocone are all present, the inner cusps being less prominent than the outer ones and the hypocone, as a younger cusp phylogenetically, smaller than the protocone. Each cusp presents a concavity open outwards. On the lateral margin of the tooth occur the parastyle and mesostyle with a vestige of the metastyle. Owing to the lateral movements in mastication the cusps of the talonid of the lower molars swing transversely through the groove between the protocone and paracone in front and the hypocone and metacone behind: apparently in association with this the mesostyle is bifid. The last upper molar presents a noteworthy feature in having a pseudohypocone. This cusp simulating the hypocone in position and appearance is observed, by comparison with less specialized members of the family, to be produced by the subdivision of the metacone. If ever a true hypocone occurred on this tooth it has been lost and a trituberculate condition restored as a specialization which may be seen in less advanced crescent-toothed Phalangers. Later in response to necessity a pseudohypocone was developed as already mentioned. The progress of evolution towards reduction of the fourth upper molar has in this case been first arrested and then actually reversed. In other words this is an instance of reversibility of evolution. In association with this the last mandibular molar is only slightly reduced in size. The cusps as in the upper teeth are crescentic but the concavity is directed inward. As in the maxillary teeth the crescents are more pronounced in the outer cusps. The paraconid is the only cusp lost. The occurrence of a slight external cingulum diminishes somewhat the notch between protoconid and hypoconid.

A selenodont adaptation of molar cusps occurs several times in the evolution of mammalian dentitions. It represents one of the inherent responses of the tooth to functional requirements and is by no means confined to a single order.

There remains another modification in which however

individual cusps are united to form crests. This is termed the lophodont dentition and will be illustrated by examples from the Kangaroos. In it the molar teeth tend to be long crowned or hypsodont whereas in both other modifications so far considered (except in *Thalacomys*) the teeth are short crowned or brachyodont.

The three types chosen to represent the lophodont dentition are the following: *Potorous tridactylus*, the common Rat Kangaroo of Eastern Australia and Tasmania (Fig. 25), *Dendrolagus inustus*, a Tree Kangaroo from New Guinea (Fig. 26),

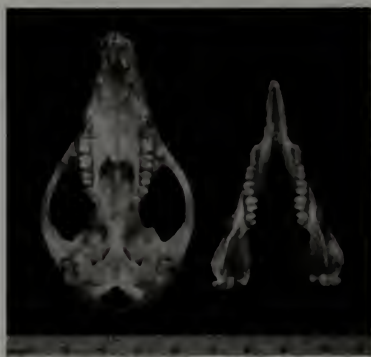


Fig. 25.—Dentition of Rat Kangaroo (*Potorous tridactylus*, 9.221-5).

and *Macropus bennetti*, Bennett's Wallaby of Tasmania (Fig. 27). *Potorous* is a nocturnal animal living in the scrub jungle and feeding on roots and bulbs as well as grass and leaves. Concerning the habits of *Dendrolagus* little is known, but it certainly feeds upon green shoots of the trees in which it lives. *Macropus* is the most advanced example and though varying its diet with shrubs and roots it is in the main a grazing animal.

Examination of the photographs shows that the dentition of *Potorous* recalls somewhat that of *Petaurus*: the other two are more specialized. Marked changes occur in all the teeth. The upper median incisors, long though not procumbent in *Potorous*, become shorter in *Dendrolagus* and equal in length the



Fig. 26.—Dentition of Tree Kangaroo (*Dendrolagus inustus*, 9.221-7).



Fig. 27.—Dentition of Bennett's Wallaby (*Macropus bennetti*, 9.221-4). Figs. 25, 26, 27 represent successive stages in the evolution of the lophodont herbivorous type ending with the grazing dentition of *Macropus*.

other upper incisors in *Macropus*. The lower incisors becoming elongated, lanceolate and more procumbent, provide, in *Macropus*, a cutting edge which works against all three upper teeth. The second upper incisors from their cramped position may become very reduced. The third incisors tend to lengthen antero-posteriorly perhaps because they have room to extend. The canines, absent throughout in the mandible, become progressively reduced in the upper jaw until in *Macropus* merely a small groove in the bone indicates their presence. The premolars vary in number with age; in the young individual the second and third are present in both jaws. As the animal grows older these two are lost though the second remains longer in *Macropus* than in the others for reasons to be specified later. In each of the examples shown the second premolar is already lost. In all but especially in the characteristically shoot-feeding form, *Dendrolagus*, this tooth shows a well marked sectorial character retained with some modification from the insectivorous-omnivorous stage.

The greatest changes are observable in the molars. The tooth rows are slightly inturned posteriorly in all three types. The molars of *Potorous* are short crowned quadritubercular bunodont teeth with slightly marked transverse ridges connecting the two anterior and the two posterior cusps. There are also ill-defined longitudinal ridges connecting the inner cusps in the upper teeth and the outer cusps in the lower teeth. The fourth upper molar shows a pseudohypocone produced as in *Phascolartos* by the division of the metacone. In *Dendrolagus* the teeth are still brachyodont but the transverse ridges with the cusps have grown prominent to form distinct crests or lophs. The antero-posterior ridge is also better marked. These features are accentuated in the most advanced type, *Macropus*, in which also the teeth are long crowned or hypsodont, the increased length residing more in the cusps (lophs) themselves than in the body of the teeth. This hypsodont character should be contrasted with the hypsodonty in the bandicoot, *Thalacomys*. The photographs of these three animals represent as

nearly as possible individuals at corresponding stages of life. But whereas in *Potorous* and in *Dendrolagus* all the molars are erupted and the first worn only slightly more than the fourth in *Macropus* the fourth is still not fully erupted although the first is greatly worn. A similar condition will be noted in the grazing Ungulates and in the Elephants. The grazing habit causes greater wear of teeth than any other form of feeding and Nature, in defense, has arranged that the hinder molars erupt later in these than in other animals and come into action as the more anterior teeth wear out. Several other features of the dentition of the Kangaroos are explicable upon the same basis. The hypsodont character of the teeth, the transformation of a bunodont into a lophodont dentition and the exaggeration of the longitudinal ridges are examples. Again whereas in *Potorous* the last molar is the smallest, in *Macropus* this tooth has become secondarily enlarged, an example of reversed evolution. In this respect *Dendrolagus* represents an intermediate stage. As the smaller but more numerous anterior teeth become worn and fall out the longer hinder teeth erupt, migrate somewhat forward in the jaw, and provide the animal with an unshortened molar row. The reasons for retention in earlier life of the second premolar in addition to the third is now clear. This tooth assists the molars before the eruption of the hinder teeth. Lastly the herbivorous Marsupials differ from insectivorous and carnivorous forms in presenting a better marked vestige of the milk dentition. All herbivorous Marsupials have a well-developed milk molar which remains in position a comparatively long time before it is replaced by the sectorial last premolar. The milk tooth thus assists the first permanent molar in function and only falls out when much worn. In *Macropus*, counting the milk molar, there are seven cheek teeth (two premolars, four permanent molars) of which, however, only three are present in old animals.

The tooth formula for the Kangaroos may now be stated but it must be remembered that these formulæ vary with age.

Potorous: $I \frac{3}{1}, C \frac{1}{0}, P \frac{1}{1}, M \frac{4}{4}$. total 30.

Dendrolagus: $I \frac{3}{1}, C \frac{1}{0}, P \frac{1}{1}, M \frac{4}{4}$. total 30.

Macropus: $I \frac{3}{1}, C \frac{0}{0}, P \frac{1}{1}, M \frac{4}{4}$. total 28.

The progressive elongation and Ungulate-like appearance of the jaws should be noted. The condyle is raised above the molars thus entailing lengthening of the mandibular ramus and narrowing of the coronoid process.

Still another animal must be included in the study of the



Fig. 28.—Dentition of Tasmanian Wombat (*Phascolomys ursinus*, 9.222-5). This animal is the only gnawing type among the Marsupials.

adaptations of the marsupial dentition, namely, *Phascolomys ursinus*, the Tasmanian Wombat (Fig. 28). It is a herbivorous animal but its dentition has taken on a gnawing character like that of the most specialized placental Rodents. It is a nocturnal burrowing creature about as large as a badger but more thickly set and feeds upon grass, other herbage and roots. The tooth formula is:

$$I \frac{1}{1}, C \frac{0}{0}, P \frac{1}{1}, M \frac{4}{4}, \text{total } 24.$$

The gnawing character is seen in the sealpriform incisors in which the enamel lies mainly upon the labial face and in the double triangular appearance of the molars which like the incisors, growing throughout life, have permanently open roots.

Nothing need be said concerning the single premolar since it resembles half a molar. The molar bodies are curved, the concavity of the upper teeth directed laterally and that of the lowers facing toward the tongue. In this way grinding pressure is not transmitted to the growing root but is supported upon the side of an arch. The crowns are worn obliquely so that the sharp edge is lateral in the upper teeth and mesial in the lower. The connected bases of the maxillary molars are lateral; those of the mandibular series mesial. The upper molars diminish in size from the second backward; in the mandible the first three molars are subequal. In both jaws the fourth molar is the smallest.

A specimen with worn teeth like the one figured does not greatly assist in the identification of the relationships of *Phascolomys*. For this a very young example is necessary. It then appears that *Phascolomys* is very like *Trichosurus* in the possession of pointed incisors and unworn molar crowns. In both there occurs the same arrangement of bunodont cusps, ridges, and ledges. Probably, therefore, *Phascolomys* had a phalangerine ancestor and its burrowing habit is secondary being readopted after a previous arboreal existence.

The peculiar condyle and coronoid process and the remarkable glenoid fossa should be noted.

To complete fully an account of the Marsupials, some reference should be made to the aberrant forms *Tarsipes*, *Myrmecobius*, and *Notoryctes*.

Tarsipes is a long snouted phalanger which, having taken to a diet of honey, exhibits a degenerate dentition. *Myrmecobius*, the Banded Anteater, is an aberrant dasyure which possesses

a very modified dentition the most remarkable feature of which is the increase in number of molars associated with degeneration of the antemolar teeth. These two peculiar diets are invariably associated with a modification of tooth form, but to avoid tedium consideration of this phenomenon will be postponed until placental Mammals exhibiting similar modifications come to be discussed (see pp. 161, 224, 271).

It will now be clear that the reason for the dominant position in phylogeny of the so-called trituberculate type of dentition is its infinite range of adaptation to meet all possible dietary conditions. The absence of this adaptability in the tooth patterns which characterize Multituberculates, Protodonts and Triconodonts is one of the factors which led to their ultimate extinction.

One peculiar modification of the tritubercular tuberculo-sectorial dentition, namely that of Notoryctes the Marsupial Mole, will be discussed in the next chapter with the very similar dentition of the Zalambdodont Insectivores.

Although full discussion of the deciduous teeth cannot be entered upon at this stage certain prominent facts concerning the marsupial milk dentition should be recalled. In this Order the milk dentition has become greatly reduced probably in consequence of the peculiar conditions of birth and of early life. In no Marsupial is there ever more than one tooth possessing a temporary predecessor. When replacement occurs it invariably involves the last premolar. The deciduous tooth is molariform and is therefore unlike its successor. The successional tooth moreover develops in front and not behind its predecessor as in the case of most replaced teeth in Placentals. The condition is therefore difficult to interpret. Possibly the deciduous tooth is really one of the permanent molar series projected as it were over the top of the posterior premolar. But whatever be the explanation the deciduous marsupial dentition illustrates very clearly the principle of reversed evolution. In the insectivorous-carnivorous series the deciduous tooth becomes progressively reduced but in the purely herbiv-

orous group this tooth apparently takes on a secondary stage of development. In the Opossums, the most primitive of all Marsupials, this tooth is well developed. It is much reduced in Phaseologale, vestigial in *Thylacinus* and absent in *Sarcophilus*. Hence it is becoming progressively eliminated though, as may be inferred from the condition in *Thylacinus* in which the last premolar is well developed and retains its primitive character, the elimination of the milk tooth is by no means necessarily paralleled by corresponding reduction in its successional tooth. The milk tooth is also vestigial in the Bandicoots, in the Koala and in the Wombat but in the Phalangers and Kangaroos (*Macropodidae*) its reduction has been arrested and indeed reversed. Apparently because of the advantage which the tooth subserves in a purely herbivorous dentition it has taken on a secondary growth in these animals and remains in place until the attainment of early adult age.

Although we have spoken of reversed evolution the expression must not be taken too literally. Evolution is irreversible after a certain stage in so far as actual structure is concerned; for example, a hypocone once lost cannot be restored. On the other hand the formation of a pseudohypocone on the last molar can result from the division of the metacone as in the Koala and the Kangaroos. Evolution is reversible in the possibility of adaptation to environment or to function. The deciduous molar becomes secondarily enlarged in the Kangaroos so as to simulate its primitive appearance in the Opossums, although the parts actually eliminated cannot themselves be regained. Further in consideration of adaptation to environment and function it must not be forgotten that the loss of a tooth, as of a digit, necessarily diminishes the plasticity of the organism as a whole in future possible adaptations.

In the adaptive radiation of the Marsupials various other principles of evolution are to be noted.

Divergent evolution is seen in the production of the molars which are bunodont in the Phalangers, selenodont or crescent-

shaped in the Koala, lophodont in the Kangaroos and columnar in the Wombat.

Parallelism is exhibited in the evolution of the molars of *Dendrolagus* and *Macropus*. These two Kangaroos are related ancestrally in the primitive bunodont stage alone but because of the inherent tendency of animal types to respond morphologically in the same manner to the same environment and life habits the lophodont dentition is strikingly similar in both.

The last mentioned principle gives some clue to the formation of species and genus. It is possible that a new species is finally evolved through similar and simultaneous modification of numerous individuals although the part played by mutations appearing in a single individual should not be underestimated. It is claimed that a new genus of South American fresh water fishes is even now in process of development through the transformation of several species of an older genus, the change going on simultaneously but independently in widely separated parts of the continent.

CHAPTER V

THE INSECTIVORES

The order to which a Mammal belongs is no real indication of its diet—Central position of the order Insectivora among placental Mammals—Dilambdodonts and Zalambdodonts—Relationship of the Tree Shrews to ancestral Primates—Parallel evolution in modern Tree Shrews and Lemurs—Convergences displayed by the Marsupial Mole and Zalambdodonts—Derivation of the Zalambdodont dentition.

In describing the dentition of the Marsupialia a fact of very great importance emerged namely that within a single order variations in dietary habit are found to be associated with differences in dentition. This should be borne definitely in mind in studying the various mammalian groups for it is easy at first to confuse the ordinal position of a Mammal with the type of its feeding habits. Among the so-called Carnivora for example the Cats are pure flesh feeders but the Dogs are omnivorous and even the most purely carnivorous Bear, the Polar Bear, varies its diet of seal with berries and grass during the short Arctic summer. One must realize therefore that the name of the order to which an animal belongs is no real guide to its customary diet. One must not infer from the foregoing description of the Marsupialia however that a complete sequence can be traced in every order commencing always with a central insectivorous or insectivorous-omnivorous form. Recent Mammals usually represent specialized and often isolated modifications from the ancestral type and it is only in the Marsupialia that a fairly complete and comprehensive sequence can be traced in existing forms. In some orders every species is now

so thoroughly specialized that only obscure traces remain to show what from the paleontological record we know its ancestry to have been but it is certain that all orders at one time or another, some in the very remote past, have originated from an insectivorous-omnivorous type.

The foregoing statement will render clear the reason for studying the Insectivores first among placental orders. Many years ago Huxley laid particular stress upon this central position of the Insectivora and announced his conviction that any one who is acquainted with the range of variation of structure in this order and in the Rodentia possesses the key to every peculiarity met with in the Primates, Carnivora and Ungulata. How true Huxley's statement has proved to be will become apparent in the perusal of the ensuing chapters.

The order Insectivora is without doubt the most ancient placental order and the animals included therein subsist upon an insectivorous diet with its usual adjuncts,—worms, reptiles, eggs, nestlings and fruit except in the case of the African Water Shrew *Potamogale* which is said to feed entirely upon fish. Animals which have preserved to the present time a phylogenetic character so ancient cannot be expected to exhibit the generalized features of their ancestors. Though certainly primitive all are exceedingly specialized and aberrant. They are sparsely distributed in the more inaccessible parts of the world or have developed some special habit of life (Moles) or some particular method of defense (Hedgehogs) whereby they are enabled better to preserve their existence.

Of the Insectivores there are two types distinct in their dentition though similar in their diet.* Of these the *Dilambdodonts* present W-shaped upper molars like those of the insectivorous *Marsupialia*, whereas the *Zalambdodonts* exhibit a peculiar triangular type of upper molar which has probably been

*This seems in direct contradiction of the general statement so often emphasized in these pages that like diets are associated with similar types of dentition even in different orders. In view of our ignorance concerning the mode and cause of evolution of the *Zalambdodont* dentition, one can only say that this, the most striking exception cannot weaken the case for the relationship in general of dentition with diet which stands self-evident (but see pp. 197, 223).

derived from the typical primitive tritubercular form through the fusion of the paracone with the metacone. Associated with the latter group from the point of view of tooth form is the curious little Marsupial Mole, *Notoryctes*.

As one of the representatives of the Dilambdodonts the common European Mole, *Talpa europea* (Fig. 29) has been chosen. The form of its molars with their needle-like cusps proclaims at once an insectivorous habit. Yet the semicircular upper in-

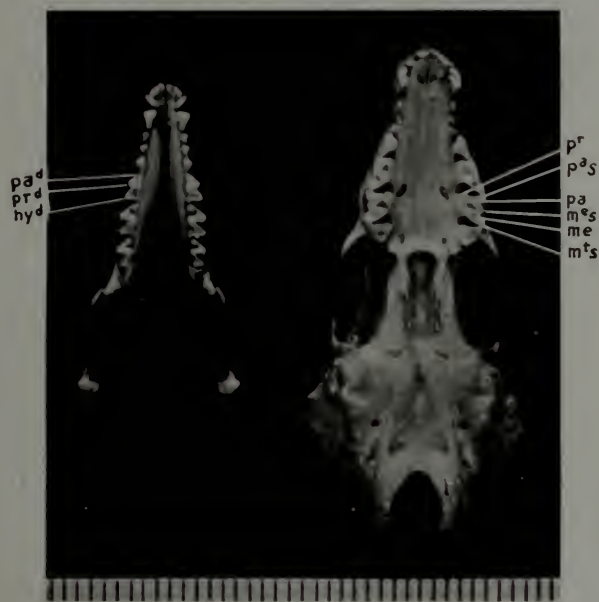


Fig. 29.—Dentition of European Mole (*Talpa europea*, 9.337-1). An example of primitive insectivorous dentition with some carnivorous adaptations.

cisor arch suggests carnivorous approximation, an adaptation further indicated by the prominent sharply pointed sectorial last upper premolar and by the shearing edge produced from the ridge connecting metacone to metastyle. The last named feature is especially obvious in the first molar. The diet of the Mole consists of earthworms, insects and their larvæ and the tooth formula is:

$$I \frac{3}{3}, C \frac{1}{1}, P \frac{4}{4}, M \frac{3}{3}, \text{total } 44.$$

This formula is important because it represents the full placental dentition. The premolars are one more and the molars one less in number than in Marsupials. Only in occasional (*Otocyon*, *Cetacea*, etc.) or in doubtful (*Shrews*) instances are these numbers exceeded. Examining the teeth in detail and comparing them with the dentition of *Phascologale* the following points may be noted. The upper median incisors show no procumbency or approximation of tips but are uniform with the others. The lower incisors are also subequal in size but are slightly procumbent. Unlike the strong upper tusk the lower canine is reduced and slightly procumbent. Associated with this is the exaggerated size of the first lower premolar. The second, third, and fourth lower premolars progressively increase in size. In the maxilla the last premolar alone attains any considerable development: it becomes a carnassial or sectorial tooth similar to but less developed than that found in *Carnivora*. The upper molars except the last show the three cusps and the three styles as in *Phascologale* but the protocone is a low shelf-like structure and projecting behind it on the first and second molars is an extension which may represent the hypocone. This is doubtful however since the cusp does not fit into the trigonid of the lower molar next behind. Into the triangular spaces between the upper teeth pass the trigonids of the lower molars in closure of the jaws. The last upper molar exhibits no metacone-metastyle shear since there is no lower tooth to occlude behind it. Each mandibular molar shows a typical three-cusped trigonid with a somewhat smaller two-cusped talonid or heel immediately behind. The talonid is reduced in the third molar. In brief then the dentition of *Talpa* as just described differs from the purely insectivorous dentition of *Phascologale* in its incipient carnivorous adaptation.

A somewhat different type of *Dilambdodont* dentition is represented in the lesser *Gymnura*, *Hylomys suilla dorsalis*

(Fig. 30), a very primitive Hedgehog from Borneo. The food of this animal so far as it is known is insectivorous; beetles, white ants and larvæ being its favorite. Quite possibly the diet is more generously omnivorous like that of its European relative. The tooth formula is the same as that of *Talpa*. The dentition shows unmistakably that the animal leans to the omnivorous rather than to the carnivorous adaptation.

The incisors, canines and premolars, though small are typ-

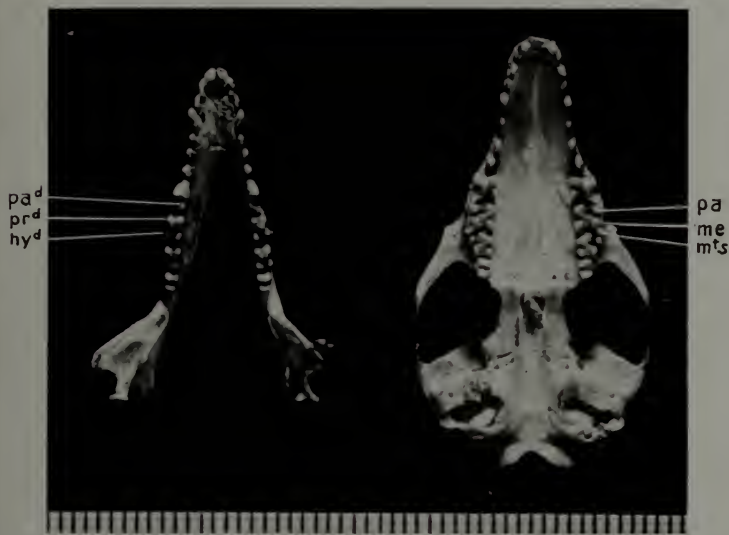


Fig. 30.—Dentition of Lesser *Gymnura* (*Hylomys suilla dorsalis*, 9.330-4). This animal retains many insectivorous features in its dentition which is adapted for an omnivorous diet.

ically insectivorous. The lower incisors are procumbent but the median uppers show neither this feature nor approximation of their tips. In each jaw the last premolar is very large and sectorial. It is the molars however to which attention is most decidedly attracted. Through reduction of the styles and the appearance of a hypocone-bearing heel the upper molars have become quadricuspid. The hypocone is well developed in the first and second but is absent in the third tooth, its place

in this being taken by an elongation of the metacone. Even in the two anterior molars the metacone-metastyle shear is greatly reduced and in the second and third it is nonexistent. The needle-like appearance of the cusps is lost and since the molars are quadrilateral there is but little space between them for the reception of the trigonid of the lower molars. In this there is a marked difference from the pattern and relations in *Talpa* and *Phascologale*. In conformity with this construction of the upper teeth the protoconid on the lower molars is greatly reduced. The protoconid-paraconid shear is found only upon the first molar. In other respects the lower teeth call for no special description. The reduction in size of the molars in both jaws from the first backward is an example of specialization. The glenoid fossa compared with that of *Phascologale* is comparatively shallow to allow for freer rotary movement in association with the omnivorous adaptation of the teeth.

Perhaps the most significant family of the *Dilambdodonts* is that of the *Tupaiaidae* or Tree Shrews which are of special importance because of their relationship to the Primates. They differ from other *Insectivora* in many features, for example, the orbit instead of being open laterally is encircled by a ring of bone as in Primates. The example chosen is *Tupaia tana*, a Bornean Tree Shrew (Fig. 31). Its diet consists of insects and fruit and the dentition is therefore insectivorous-omnivorous. The tooth formula is:

$$I \frac{2}{3}, C \frac{1}{1}, P \frac{3}{3}, M \frac{3}{3}, \text{ total } 38.$$

The third upper incisor and the first premolar of both jaws in the ancestral dentition have been lost. The markedly procumbent lower incisors, the reduced upper canines and the increase in size backward of the premolars are noteworthy. The upper molars except the last show the styles plainly although the metacone-metastyle shear is absent. The hypocone is more developed than in *Talpa* but less pronounced than in *Hylomys*. Each lower molar shows a small but distinct para-

conid. The molar teeth of both jaws show the specialized feature of decrease in size from the first backwards. The glenoid fossa is broad antero-posteriorly and shallow in conformity with the omnivorous type of dentition.

In general then the teeth of *Tupaia* exhibit a tendency toward the omnivorous adaptation less pronounced than that of *Hylomys*. But *Tupaia* is an advanced type. Its ancestry can be traced back to the Eocene of North America in which occurs

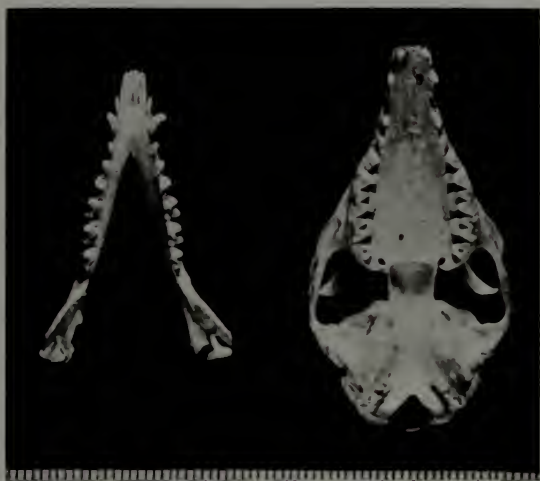


Fig. 31.—Dentition of Bornean Tree Shrew (*Tupaia tana*, 9.331-1). An animal of special significance because of the relationship of its ancestry with that of the Primates.

a Tupaiid, *Entomolestes*, the primitive characters of which indicate that it lies close to the point of divergence between modern Tree Shrews and non-Malagasy Lemurs. From this we must infer that although in skull, skeleton and dentition, *Tupaia* resembles the Lemurs quite closely it has attained the Lemur-like features independently by parallel evolution. In the study of teeth and skull there is often noted a tendency in different orders or families towards evolution along parallel lines, a tendency of very great importance which cannot be too often emphasized.

In a work of restricted size many important types must necessarily be omitted. It would be inexcusable however to pass over the Zalambdodonts without at least some reference, although for obvious reasons they cannot be fully considered. With these animals should be grouped the Marsupial Mole, *Notoryctes* which presents a similar type of dentition.

A specialized representative of the Zalambdodonts is *Chrysochloris trevelyani*, the largest of the Cape Golden Moles (Fig. 32). This fossorial animal belongs to a family which is



Fig. 32.—Dentition of Cape Golden Mole (*Chrysochloris trevelyani*, 9.335-1). A representative of the most primitive type of living Mammals.

probably more primitive than any other group of Mammals now living. So far as is known its food consists mainly of earth-worms but the dentition differs greatly from that of other Moles although paleontology shows it to have been derived probably from the same stock as the Dilambdodonts. The tooth formula is:

$$I \frac{2}{2}, C \frac{1}{1}, P \frac{4}{4}, M \frac{3}{3}, \text{total } 40.$$

The upper median incisors are nearly vertical but are large and their tips approximate. This, together with the inflection

of the mandible gives the skull a superficial resemblance to the Marsupials which however is not confirmed upon further study. The canines are reduced and the last premolar in each jaw is completely molariform. The last molar is greatly reduced as would be expected in so specialized an animal and in each jaw the first molar is the largest of the three. The upper molars are triangular, compressed from before backward and elongated from side to side. There is a single internal cusp flanked on its palatal side by a well-marked cingulum. Laterally placed are two cusps, the homologies of which are obscure. The lower molars also are triangular, having on the labial aspect the apex formed by a tall cusp, the protoconid. On the lingual side are two cusps, paraconid and metaconid which are related to the protoconid almost as in typical Jurassic Trituberculates. On the distal or posterior face of the tooth is a small spur-like heel. The lower molars fit between the upper teeth and thus form well-marked shears.

The inference to be drawn from examination of the teeth of the Zalambdodonts is that they must be considered apart from more truly tritubercular tuberculo-sectorial dentitions exhibited by other Mammals. The Marsupial Mole either is derived with the Zalambdodonts from a remote common ancestor or has attained the very specialized features of its dentition by convergence.

Gregory's most recent attempt to homologize the cusps of the teeth in *Chrysochloris* depends upon a modified conception of the Premolar Analogy Theory. Suffice it to observe that the first permanent molar quite possibly belongs in reality to the milk dentition, whereas the permanent premolars belong to the successional set. Looked at from this standpoint precise homologies of the cusps of the permanent molars must not be sought directly in the premolars but in the milk molars (see Fig. 77). It is known that the first cusp to develop in the upper molar is the paracone and that the protocone develops later: hence it is probable that the paracone is phylogenetically the older cusp and that it represents the apex of the primi-

tive simple reptilian tooth. In its turn the main cusp of the premolar has the same homology and thus corresponds with the molar paracone. In *Chrysochloris* the upper molar cusp which occupies the site upon the crown in series with the main cusp of the premolars is the palatal cusp at the apex of the triangle. This should then be the paracone and the cusps at the base of the triangle represent the external styles: the palatal cingulum corresponds to the protocone. This type of tooth dates back almost unchanged to the Oligocene (*Apter-*



Fig. 33.—Dentition of West African Water Shrew (*Potamogale velox*, 9.333-1). The dentition of this animal stands intermediate between those of the more typical Insectivores and that of the very specialized form *Chrysochloris*. A milk tooth is retained in this specimen among the upper premolars. The shadow falls so densely between the trigonids of the mandibular molars that the heel or talonid can be seen upon the last one only.

nodus) and it may be that the metacone like the hypocone never formed. Further light upon the derivation of this type of molar is shed however by *Palaeoryctes*, a very ancient Mammal occurring in the Paleocene. In this the paracone and metacone are very close together as if the latter had just budded off the former.

Potamogale velox, the West African Water Shrew (Fig. 33),

an animal aberrant in many details and adapted it is said for a fish diet, exhibits a dentition very similar to that of the primitive Palaeoryctes and thus supplies an indication of the correlation between the teeth of the Zalambdodonts and Dilambdodonts. The tooth formula is:

$$I \frac{3}{3}, C \frac{1}{1}, P \frac{3}{3}, M \frac{3}{3}, \text{total } 40.$$

The specimen figured has retained the first milk cheek tooth in the upper jaw but it is a very useful specimen since the last premolars are just erupting and all cusps are clearly shown. In general the dentition and the shape of the dental arch are of the usual insectivorous type and the last two premolars in each jaw are increasingly molariform. Each mandibular molar shows a typical trigonid with all three cusps and a heel of fair size but low. In the upper molars a cusp not found in *Chrysochloris* appears behind and slightly lateral to that at the apex of the triangle on the palatal aspect. It is best marked on the second molar. If the cusp at the apex be the paracone this one must be the metacone either just budded off from or fusing with the paracone. The very ancient and very specialized nature of the Zalambdodont group renders difficult exact comparison with the cusps of the teeth in other mammalian forms.

CHAPTER VI

THE PRIMATES (EXCEPT MAN)

General features of the order—Its Eocene history—Tarsiidae and Adapidae—The Lemurs—Recent change of life habits in *Lemur catta*—Extreme Rodent adaptation in Aye-aye—Parallel evolution in Primates—Importance and early occurrence of reduction in incisor series—Herbivorous adaptation in some New-World Monkeys—Ancestry of Old-World Monkeys and Apes—*Parapithecus*—Commencing herbivorous adaptation in *Lasiopyga*—Completely herbivorous forms—*Papio*—The Langurs and Guerezas—Ancestors of the Anthropoids—Position of the modern Gibbons—The black Anthropoids, Gorilla and Chimpanzee—The red Anthropoid, Orang—Frugivorous adaptation in Orang—Summary of features of the Anthropoid dentition.

The Primates, a varied assemblage of Mammals, most of them arboreal in habit, are especially interesting since the order includes Man himself. Our closest relations are the great Anthropoids, the Gorilla, the Chimpanzee and the Orang. Further removed is the small Anthropoid, the Gibbon. The Old-World Apes and Monkeys represent a more distant branch of Primate stock but further still removed are the American Monkeys. The Lemurs, for the most part highly specialized and even retrogressive, stand so distinctly by themselves that many authors deny their right to inclusion within the order.

In studying these animals it is quite important to remember that they do not represent a steady succession with Man himself as the culmination but each family having derived its origin from some primitive ancestor has specialized along its own line which however has run more or less parallel during

the ages with the lines of specialization of other families. It is usual to consider Man as the topmost twig of the phylogenetic tree while other twigs on lower planes and perhaps further removed from the trunk represent other members of the Primate stock. Yet it is perhaps not quite exact to speak of Man as at the top unless one understand thereby a relatively steady evolution in Man's history with the maintenance of a still largely generalized structure even at the present day.

Except for certain fossil representatives occurring before the Primate line of evolution was thoroughly established all members of the order are readily distinguishable, though details of the distinctive features lie beyond the compass of this work. It may be mentioned in passing that with the exception of certain Lemurs, all Primates present two upper and two lower incisors and further that the orbit possesses at least a complete ring of bone separating it from the temporal fossa. The dental formula is very generally:

$$I \frac{2}{2}, C \frac{1}{1}, P \frac{3}{3} \text{ (or } P \frac{2}{2} \text{)}, M \frac{3}{3}, \text{ total } 36 \text{ (or } 32 \text{)}.$$

Within the order are to be found, originating from a central insectivorous-omnivorous type not unlike that of the Tree Shrews, several forms of dentition adapted for frugivorous or for herbivorous diet or even for the extreme gnawing habit. Though many species will and do eat flesh, none is entirely carnivorous. It is not along the purely flesh-eating line but in the herbivorous direction that we find evolution of the Primate dentition. The general principles of this adaptation have already been set forth in the chapter on Marsupials so that the student may be expected to be familiar with them. It will thus be an easy matter to note the increasing specialization of each family discussed.

It is not possible to utilize modern Primates to illustrate progressive evolution so readily as it was in the case of the Marsupials, for the order Primates does not contain among its existing representatives so comprehensive a series of tooth

forms. The various families diverged from one another very early and of each there is now living only a scattered remnant. It is quite necessary to turn to paleontology to learn exactly what was the general method of evolution. For this purpose the early history of any family will serve provided it is fairly satisfactorily known. One of the modern species which will be figured later is the Specter-lemur *Tarsius* and the paleontological history of the family to which it belongs will serve as an example.

In Eocene times, as Dr. Matthew has shown, the various genera of Tarsiidae present a fairly uninterrupted succession. In the earliest species the mandible is slender with gently procumbent incisors and a moderately large canine. There is no crowding of the premolars; and the molars, in spite of the fact that the talonid is already large, show a well-marked paraconid. The last molar is unreduced. In the upper jaw the premolars are bicuspid and the molars present a typical trigon with no external styles and but an incipient hypocone. The last upper molar is somewhat smaller than the others and shows no hypocone. The dental formula is:

$$I \frac{2}{2}, C \frac{2}{1}, P \frac{3}{3}, M \frac{3}{3}.$$

In later species the mandible becomes short and deeper and the small incisors more vertical though the canine retains its moderate size. The premolars are rather crowded and the molars become shorter with the paraconid showing signs of retrogression although the last lower molar is still unreduced. From these species it is known that the upper incisors numbered two and that there was an upper canine. In still later species the shortening and deepening of the mandible are more marked, the premolars more crowded, and the molars yet shorter with the paraconid more vestigial. The last lower molar however remains long. In the most recent Eocene group at present known the mandible is very short and very

deep, the paraconid remains in greatly lessened size and the last molar is reduced.

Early features of the Primate stock are then a short and deep mandibular body with vertical incisors, a moderately large canine, crowded premolars, and molars showing in the mandible a large talonid and a reduced paraconid and in the maxilla a simple trigon with an incipient hypocone but no styles. In addition the last upper molar is only slightly reduced and the last lower not at all. But even this primitive stage shows some deviation from the common ancestral insectivorous Mammal. Both incisors and premolars are less in number and in the molars the talonid is already pronounced.

Earlier stages in the phylogenetic history of the Eocene Primates are illustrated in another extinct family of the Lemurs, namely the Adapidae. In these the dental formula was:

$$I \frac{2}{2}, C \frac{1}{1}, P \frac{4}{4}, M \frac{3}{3}.$$

In the more primitive species the premolars are only slightly or not at all bicuspid and the upper molars have no hypocone. In more advanced forms the upper molars show the beginning of style formation.

The loss of one incisor must have occurred at the very commencement of Primate evolution whereas the loss of premolars occurred later and has been progressive. Certain other primitive features of the Primate mandible are the divergence backward of the limbs of the dental arch, the absence of an "ape-shelf" and the lack of bony deposit on the inner side of the mandibular body in the region of the anterior teeth.

THE LEMURS

The Lemurs, undoubtedly the lowest group of the Primates, are now represented by a number of highly specialized and more or less degenerate species which, however, in spite of divergences characteristic of the group, illustrate the trend of progress in the dentition general to the Primates.

Tarsius, already mentioned, the Specter-lemur of the Malay Archipelago (Fig. 34), though specializing from the main ancestral stock very early, still retains certain quite primitive features. The dental formula is:

$$I \frac{2}{1}, C \frac{1}{1}, P \frac{3}{3}, M \frac{3}{3}, \text{total } 34.$$

Despite the marked change in the incisor region the molars retain their subequal size (indeed the last lower molar is even longer than the others), the upper molars possess no hypocone

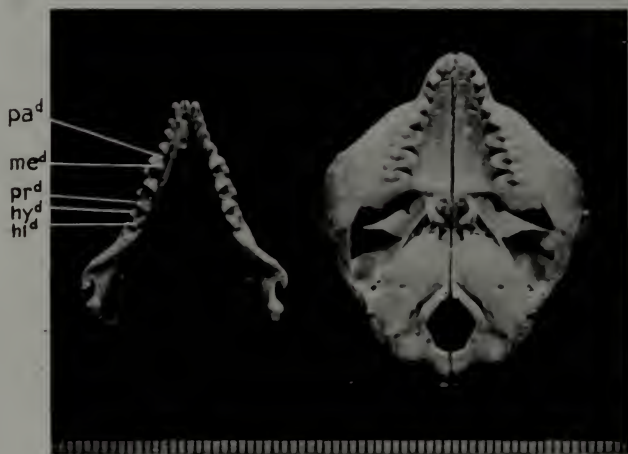


Fig. 34.—Dentition of Specter-lemur (*Tarsius borneanus*, Elliot; 9.816-1). This Lemur exhibits very primitive features in the molars although the incisor region has undergone marked specialization.

but merely a low cingulum on the palatal aspect of the protocone, and each lower molar exhibits a paraconid while the third has a large median hypoconulid. The retraction of the incisor region, normal for all Primates, has been carried further than usual in *Tarsius* but there seems to have been no marked crowding in the molar area. The divergent limbs of the dental arch and the extension of the palate somewhat behind the last molars are, like the pointed premolars, primitive

characters. The canines are reduced in size. The diet of *Tarsius* is not certainly known but captive animals will eat grasshoppers and drink milk out of a spoon. So far as information goes the diet is insectivorous although the cusps of the teeth are less sharp and more rounded than usual in insectivorous Mammals.

Another small Lemur, *Microcebus murinus*, the Mouse-lemur (Fig. 35) of Madagascar belonging to a different family shows pronounced lemuroid peculiarities, though at the same time it



Fig. 35.—Dentition of Mouse-lemur (*Microcebus murinus*, Miller; 9.813-1). This dentition shows some advances upon that of *Tarsius* in the incipient hypocone and the loss of the paraconid. It is not so specialized as that of *Tarsius* in the incisor region.

represents a primitive stage in evolution of the Primate dentition. Its food consists of insects, fruit and perhaps honey. The dental formula is:

$$I \frac{2}{2}, C \frac{1}{1}, P \frac{3}{3}, M \frac{3}{3}, \text{total } 36.$$

The very procumbent lower incisors and canines are typically lemurine and are said to be used as a comb for the fur.

The approximating tips of the upper median incisors and the fenestration of the palate are marsupial-like but the student should not mistake the animal for a Marsupial. The upper canine is not prominent and the last upper premolar is bicuspid. The upper molars, subequal in size, show a trigon similar to that of *Tarsius*, but in addition, there is an incipient hypocone upon the internal cingulum in the first and the second molars. In association with this the lower molars have lost their paraconid and in all of them the metaconid lies upon a plane somewhat distal to the protoconid, a situation primitive in Primates. The hypoconulid on the last lower molar is large.

Lemur catta, the Ring-tailed Lemur of Madagascar (Fig. 36), is a much larger animal than *Microcebus* but more retrogressive. It is a species which has recently (geologically speaking) forsaken an arboreal existence for a life among the rocks and stunted bushes. Its principal food is now the prickly pear probably supplemented in the summer by bananas and figs. It will not eat meat. It is perhaps because this change in diet is of recent occurrence that the dentition shows insectivorous-omnivorous features, although certainly more degenerate than those of *Microcebus*. The dental formula is the same but the teeth exhibit many specialized and retrogressive characters. The upper incisors are vestigial, the lower first premolar increasingly caniniform, the internal cingulum of the first and second upper molars is now represented by two tubercles, one in front (Carabelli's tubercle, see page 161), the other behind the protocone. The last upper molar is the smallest, the first and second are subequal. The hinder ends of the elongated upper dental arch are much less divergent than in *Microcebus* and the palate does not extend back to the third molar. In the mandible the third molar is the smallest, lacks the hypoconulid and its axis tends to converge backwards toward that of its fellow.

The purely herbivorous Lemurs or Indrisinae all exhibit crescentic cusps on the molars, but like other Lemurs are a degenerate and specialized group. As a representative species we

will consider *Lichanotus laniger*, the Woolly Lemur of Madagascar (Fig. 37), the tooth forms of which may profitably be compared with those of *Tupaia*. Regarding the habits of this nocturnal animal little is known but it is probable that its diet like that of its nearest relations, the Sifakas, consists of leaves, fruits and flowers. The tooth formula is probably best represented thus:

$$I \frac{2}{1}, C \frac{1}{1}, P \frac{2}{2}, M \frac{3}{3}, \text{total } 30^*.$$

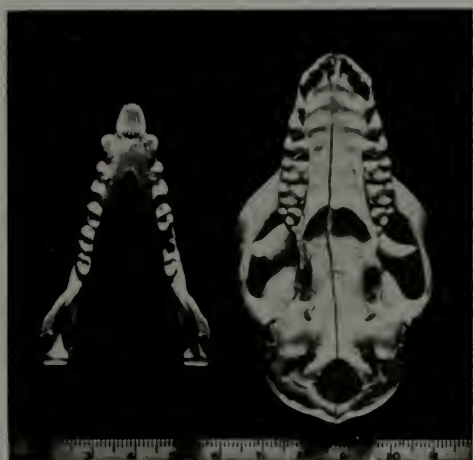


Fig. 36.—Dentition of Ring-tailed Lemur (*Lemur catta*, Linnaeus; 9.812-3). This animal having only recently changed its mode of life and feeding habits has not yet developed any marked resulting changes in its dentition.

The decrease in size backward of the upper molars, the convergence backward of the limbs of the upper dental arch and the extension of the palate no further than the middle of the second molar all indicate specialization. So also do the rudimentary upper incisors, the premolariform condition of the upper and the incisiform appearance of the lower canine together with the loss of the second lower incisor. It is noteworthy that in the last upper molar the metacone has subdivided to form a pseudohypocone, probably in association

with the type of diet, thus recalling the condition in the marsupial Koala. The paraconid has disappeared from each of the lower molars and the third presents only a small hypoconulid but although very specialized there are traces left of a primitive feature in the occurrence on the first and second upper molars of the three outer styles which are utilized as in the Koala for the conversion of paracone and metacone into crescentic cusps. Indeed the molars of the purely herbivorous



Fig. 37.—Dentition of Woolly Lemur (*Lichanotus laniger*, Gmelin; 9.811-2). This purely herbivorous Primate presents crescent-cusped molars. The upper incisors have been lost in the specimen but their sockets are plainly seen and indicate the vestigial nature of the teeth. Compare this figure with Fig. 24.

lemur and the correspondingly herbivorous Koala present a striking instance of convergent evolution. The general pattern of the molars of *Tupaia* affords an indication of the type from which the molars of *Lichanotus* originated.

The most aberrant of the Indrisinae is the rodent-like Aye-

*The dental formula of the Indrisinae is in dispute. Some give it thus:

$$I \begin{smallmatrix} 2 \\ 2 \end{smallmatrix}, C \begin{smallmatrix} 1 \\ 0 \end{smallmatrix}, P \begin{smallmatrix} 2 \\ 2 \end{smallmatrix}, M \begin{smallmatrix} 3 \\ 3 \end{smallmatrix}, \text{ total } 30.$$

Such an interpretation would indicate that the lower incisiform tooth in *Daubentonia* is really an incisor.

aye, *Daubentonia madagascariensis* (Fig. 38) a peculiar and little known creature which lives in the dense forests and bamboo brakes of Madagascar. Its food consists probably of grubs, plant juices and fruits, the two former being extracted after the powerful incisiform teeth have torn off the bark. The two halves of the mandible, as in the Kangaroo, can be separated somewhat and thus allow a little space between the chisel-like teeth. The dental formula is probably best represented thus:

$$I \frac{1}{0}, C \frac{0}{1}, P \frac{1}{0}, M \frac{3}{3}, \text{total } 18.$$

The front teeth of both jaws are long, curved and possess persistent pulps. As in Rodents the enamel is largely upon the



Fig. 38.—Dentition of Aye-aye (*Daubentonia madagascariensis*, Gmelin; 9.815-1). Note the rodent-like front teeth and the degenerate and much worn cheek teeth. The whole skull is modified in accordance with the dental specialization.

labial face of the teeth. From these the cheek teeth are separated by a long interval. They have not persistent pulps like the front teeth but present true roots and are plainly very degenerate with obscure cusps. The absence of convergence

of the hinder ends of the upper dental arch and the extension of the palate as far back as the last molar are of course accounted for by the narrowing of the entire palate and the small size of the degenerate cheek teeth. The milk dentition of this animal is much more lemurine than the permanent set. The Aye-aye in fact is a remarkable instance of convergence in evolution. In Madagascar as in Australia there are practically no Rodents. In the one island the Aye-aye and in the other the Wombat takes their place and presents similar modifications in its dentition.

In general the Lemurs are a most interesting suborder for they show excellently many variations possible in dentition following changes in life habits and in diet but all originating from a single central type. The modern representatives of the suborder though widely distributed from Africa through India to the Malay Archipelago are very definitely divided into two groups, the Malagasy and non-Malagasy. These two groups have evolved along parallel lines but have been separated from each other ever since Madagascar was cut off from Africa at the base of the Tertiary. Existing forms are very specialized and largely decadent as already stated.

In the evolution of the Lemurs there has been a gradual loss of premolars until only the third and fourth of the original series remain for whereas the extinct Adapidae possessed four premolars, the majority of living Lemurs have but three and the Indrisinae only two. There is no doubt that a similar process of reduction has occurred in the Monkeys and Apes.

It is instructive to note that among the Indrisinae there has been a type now extinct but represented during the Pleistocene by the species *Paleopropithecus* in which the dentition was adapted for a purely herbivorous diet and which considerably resembled in consequence that of modern Baboons. This is another instance of parallel evolution.

In the Primates reduction in the number of incisors took place very early; reduction in the premolar series occurred later and probably more slowly. Among the Anthropeidea

(Monkeys and Apes) we find successive reductions in the premolar series. In the American Monkeys the premolar formula is:

$$\frac{3}{3}$$

but in all Old-World Monkeys, in Anthropoids and in Man it has become:

$$\frac{2}{2}$$

THE AMERICAN MONKEYS

Little is known concerning the ancestry of the New-World Monkeys (Platyrrhinae) and as they are an off-shoot of the main Primate stock they will be only briefly considered. The two families are the Hapalidae or Marmosets and the Cebidae which comprise all other varieties. The Hapalidae differ from the other family in having only two molars in each jaw instead of three. The members of this family are very specialized and retrogressive. Of the Cebidae two examples are presented, the first showing an omnivorous dentition and the second a purely herbivorous adaptation.

Ateles belzebuth, the white bellied or "Mexican" Spider-monkey from the region of the Orinoco (Fig. 39), feeds upon a mixed diet of insects, eggs, birds and fruit and presents a fairly typical omnivorous dentition. The formula is:

$$I \frac{2}{2}, C \frac{1}{1}, P \frac{3}{3}, M \frac{3}{3}, \text{total } 36.$$

Its specialized position is indicated by the termination of the palate at the level of the second molar and by the almost parallel limbs of the dental arch. The incisors of both jaws are gently sloping; this is not a primitive character but pseudo-primitive having been adopted comparatively recently. The canines are of moderate length and the premolars, especially those of the maxilla, are bicuspid. All these features, as pre-

viously noted, indicate progression. The molars of both jaws decrease in size from the first to the third and their crowns are rhomboidal with a somewhat rounded contour, characters similar to those of the human molars and attained as the result of parallel evolution. In the upper series there is a well marked trigon and a pronounced hypocone. An oblique ridge connects the protocone with the metacone as in Anthropoids and in Man. In the lower molars the paraconid is lost and the



Fig. 39.—Dentition of White-bellied Spider-monkey (*Ateles belzebuth*, E. Geoffroy; 9.882-2). The left upper incisors are wanting. Note the rounded molar crowns and the presence of an oblique ridge on the upper molars.

metaconid extends its base as far forward as that of the protoconid with which cusp it is connected in the first and second molars by a low transverse ridge. The talonid is large and basin-shaped and possesses a small hypoconulid.

In contradistinction to the omnivorous characters of the dentition of *Ateles* are the purely herbivorous features of the teeth in *Alouatta*, the Howler (Fig. 40), an animal the diet of which is stated to consist entirely of leaves. The dental formula is the same as in *Ateles*.

Alouatta is also a specialized type although the hinder margin of the palate in this animal has traveled backward. The mandible presents a striking feature in the enormous expansion of the body at its junction with the ramus. There is also considerable restriction of the interdental space as far back as the first molar by the deposit of bone on the inner aspect of the jaw. The small incisors, both upper and lower, slope forward as in *Ateles*. The canines are large. The premolars

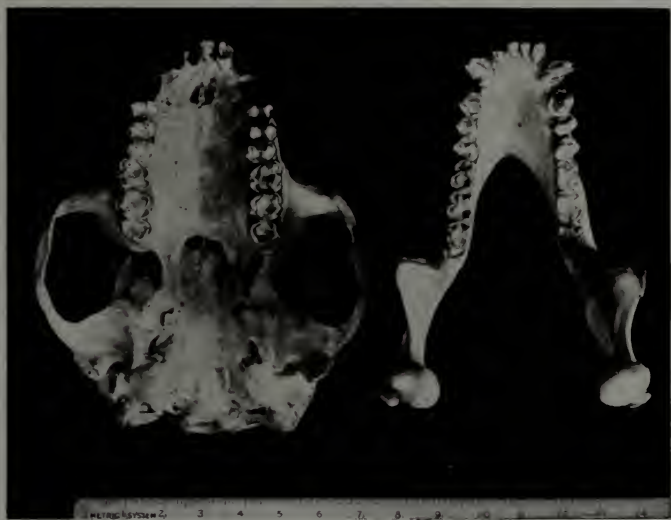


Fig. 40.—Dentition of Howler (*Alouatta palliata*, Gray; 9.822-1). The crescent-cusped molars of this dentition should be compared with those of *Lichanotus* (Fig. 37). The upper incisor and canine series is imperfect in this specimen.

are bicuspid and in the mandible the first is larger than either of the other two. In the upper molars which slightly decrease in size from the first backward, the pronounced character of the external cingulum and the development of a mesostyle combine to provide the teeth with crescentic cusps concave outward like those of the marsupial Koala. It will be recalled that the diet of the Koala consists almost wholly of leaves. A resemblance between the lower molars of these two animals is

also to be noted. In *Alouatta* the lower molars are subequal in size and elongated from the presence of a large talonid. The protoconid and hypoconid are well-developed cusps which by continuation into the anterior and posterior bounding ridges respectively of the tooth become crescentic, the concavity of the crescent being directed inward. As in *Ateles* the paraconid is lost and the metaconid has extended forward. Another feature associated in *Alouatta* with the purely herbivorous diet is the upward extension of the mandibular ramus which brings the condyle to a level far above that of the molar teeth.

If reference now be made to the marsupial dentitions of the *Phalanger* (page 82) and the *Koala* (page 83), it will be seen that in their cheek teeth patterns these resemble in general the dentitions of *Ateles* and *Alouatta* respectively, since similar food habits tend to call forth corresponding modifications in dentition, especially in the molar series, of animals belonging to widely different orders.

THE OLD-WORLD MONKEYS AND APES

All existing Old-World Monkeys are specialized. Hence to render the successive adaptation more intelligible the earliest and most primitive species yet discovered, namely *Parapithecus*, is introduced (Fig. 41). This animal lived in Egypt during the Oligocene and is known from the mandible alone. The jaw presents a superficial resemblance to that of *Tarsius*. Indeed the same dental formula has been given to both though it now appears that the formula for *Parapithecus* should read:

$$I \frac{2}{2}, C \frac{1}{1}, P \frac{2}{2}, M \frac{3}{3}.$$

The resemblance alluded to is not confirmed on closer investigation and this is scarcely remarkable for *Tarsius* is a modern type specialized in many respects whereas *Parapithecus* is an early and more generalized form.

Parapithecus possesses a short mandible and a dental arch with divergent limbs, features so characteristic of the more generalized early Primates. The jaw however is not deep and there is marked obliquity of the symphyseal region. In these features and in the characters of the teeth the animal cannot be called primitive. The canines are greatly reduced and the third molars are also small. All the molars have lost the paraconid. In the second and third mandibular molars the protoconid lies more anteriorly than in the Lemurs or in Eocene Primates. The molar cusps are rounded and incipient



Fig. 41.—Mandibular dentition of *Parapithecus fraasi*, Schlosser (from cast by Krantz, 9.823-12). An Oligocene omnivorous ancestor of modern Old-World Monkeys. The specimen shows that already some specialization had occurred in the Old-World line.

ridges connect the protoconid with the metaconid and the hypoconid with the entoconid. Notwithstanding these features the dentition in *Parapithecus* shows less specialization than the teeth of modern Old-World Monkeys.

The dentition of *Parapithecus* as just outlined is adapted for an omnivorous diet. From this there have developed in more recent times dentitions increasingly herbivorous or frugivorous in type. As examples of progressive adaptation the Mona Monkey and the Arabian Baboon are taken but it must be clearly understood that these animals are in no way closely

related and certainly the one is not derived from the other. Their dentitions compared with each other and with that of *Parapithecus* however show the general line of progress in the dentition of Old-World Monkeys in all of which the dental formula is:

$$I \frac{2}{2}, C \frac{1}{1}, P \frac{2}{2}, M \frac{3}{3}, \text{total } 32.$$

Lasiopyga mona, the pretty Mona Guenon of West Africa



Fig. 42.—Dentition of Mona Guenon (*Lasiopyga mona*, Schreber, 9.823-1). Example of omnivorous dentition with a tendency toward the purely herbivorous adaptation.

(Fig. 42), although feeding largely upon fruits, leaves and honey still retains a taste for fledglings and eggs. One finds its dentition, therefore, though progressing considerably beyond that of *Parapithecus* along the herbivorous line, less specialized than that of the Baboon. Compared with that of *Parapithecus* the mandible of *Lasiopyga* is secondarily elongated and the limbs of the dental arch instead of being divergent

are parallel, even approximated at the level of the last molar. The symphysial region is fairly well filled up with bony tissue. The palate extends as far back as the last molar. The incisors of both jaws are gently procumbent. There is a great increase in length of the canines different in type from that found in Carnivora and suggesting another rôle. The upper canine is much longer than the lower and is peculiarly twisted so that the teeth do not interlock as in the pure flesh-feeder. This elongation of the canine is partly sexual and defensive but its special character is indicated by the peculiar formation of the first lower premolar. This tooth is sectorial in appearance and, being tilted backwards, presents a covering of enamel well down its anterior root. It is obvious that the upper canine, shearing between the adjacent edges of this tooth and the lower canine will have great piercing and cutting power very advantageous in biting roots and fruits which possess a thick and tough rind. This adaptation of the canines and the first lower premolar is very common among modern Old-World Primates and indeed is one of their chief specializations. The second mandibular premolar inclines to a molariform appearance; the two upper premolars are simple bicuspid teeth. Certain markedly progressive features are present in the molar series. In both maxilla and mandible the first molar is the smallest and though the third is the largest in the lower jaw the second is somewhat bigger than the third in the maxillary series. Transverse ridges are apparent on the molars of both jaws and the cusps are rather long. In the upper molars the hypocone is a large cusp connected with the metacone by a ridge.* In the lower molars the paraconid is missing and the metaconid is placed well forward and connected with the protoconid by a ridge. The talonid is large but presents no hypoconulid even on the third molar.

There is still further specialization in the dentition of the purely herbivorous Baboon. *Papio hamadryas arabis*, the

*The *oblique* ridge connecting protocone with metacone is found only in the Anthropoids among Old-World non-lemurine Primates.

Arabian Baboon, the dentition of which is presented in Fig. 43, feeds solely upon roots and berries. The pronounced elongation of the jaws which has plainly occurred after the premolars had become reduced in number gives the animal a dog-like appearance and has resulted in actual convergence backward of the limbs of the dental arch. In the mandible the interdental space is very narrow, the symphyseal region being largely filled up with bone. Sloping incisors, enormous ca-



Fig. 43.—Dentition of Arabian Baboon (*Papio hamadryas arabicus*, Thomas; 9.823-5). Example of a purely herbivorous Primate dentition. Compare the molars in this figure with those of the Pig (Fig. 72). Note the secondary elongation of all the molars but especially of the lower third.

nines and a typical Primate sectorial first lower premolar are again obvious, the last-mentioned being especially well marked. The molars are strikingly developed; they increase in size from first to third in both jaws and the transverse ridges joining the high nipple-shaped cusps are very pronounced. The last lower molar is considerably lengthened by the occurrence upon its talonid of a large hypoconulid. Altogether the dentition of

Papio presents a swine-like appearance which can be explained as the result of a similar diet.

We have used Papio as the type of all more specialized Old-World Monkeys including the Macaques. Like Lasiopyga this animal belongs to the subfamily Lasiopyginae (Cercopithecinae. Had space permitted it would have been possible to show precisely the same progressive features in the other subfamily, namely the Colobinae (Semnopithecinae), which comprises the Langurs and Guerezas.

THE ANTHROPOID APES

Like the Old-World Apes the modern Anthropoids are all specialized and in order to evaluate correctly the various features of their respective dentitions it is essential first to note the dental characteristics of earlier forms. For this purpose we shall turn to the Oligocene Primate Propliopithecus.

Propliopithecus (Fig. 44), known only from the mandible, was discovered in Egypt and probably is the direct ancestor of all the higher Anthropoids and even of Man himself. The teeth and jaw undoubtedly reveal the primitive features characteristic of the early Anthropoid stem. Both body and ramus of the mandible are stout and the former presents the depth so distinctive of the higher Primates. The symphysial region is much less sloping than in Parapithecus. The ramus is very broad and gives a large area of attachment for the masseter and internal pterygoid muscles whereas that for the temporal is strikingly small. The muzzle was short, not elongated. There is no "ape-shelf" projecting backward from the symphysis into the tongue space which itself is relatively large and well hollowed-out.

Though the incisors are not certainly known it is probable that they were small and almost vertical. The canine is low-crowned but strong and vertical. The first premolar shows none of the special features already noted as characteristic of the fruit, rind and root cutting dentition. The second premolar

is a bicuspid tooth. The three molars are subequal in size but the posterior moiety (talonid) of the third is relatively narrower and longer than in the others.

In all the molars the paraconid is lost and the hypoconulid which is present tends to lie toward the inner side. All the cusps are low and rounded and incipient crests connect the protoconid with the metaconid and with the hypoconid. The last-mentioned is the largest cusp and it is important to note that its base, joining that of the relatively large metaconid, sepa-



Fig. 44.—Mandibular dentition of *Propiopithecus haeckeli*, Schlosser (from cast by Krantz, 9.88-17). An Oligocene omnivorous ancestor of the anthropoids.

rates the protoconid from the entoconid. The molars are not rhomboidal as in *Parapithecus* but rather oval with the antero-posterior diameter very little greater than the transverse. The basin-like crown is hollowed for the reception of the protocone of the upper molar. From these features we may infer that the skull had a short stout muzzle, that the area for the temporal muscle was small, the upper canine short, the premolars bicuspid and that the molars each presented a typical trigon with the addition of a hypocone. The formula of the mandible is:

$$I \frac{1}{2}, C \frac{1}{1}, P \frac{2}{2}, M \frac{3}{3}.$$

The dentition is certainly not yet adapted for a pure fruit or root diet but is that of a more generally omnivorous animal.

Turning now to the modern Anthropoids we find both large and small varieties. The small Anthropoids or Gibbons are animals weighing about 17 lbs. when adult. The large Anthropoids are as heavy or heavier than Man. The dental formula in all is:

$$I \frac{2}{2}, C \frac{1}{1}, P \frac{2}{2}, M \frac{3}{3}, \text{ total } 32.$$

The Gibbons (*Hylobates*) are widely distributed over Further India and the Malay Archipelago. They are light arboreal apes with disproportionately long arms by means of which they swing themselves from branch to branch. Among the numerous species considerable variations occur in teeth and jaws. Differences are to be found also between members of the same species and of the same sex.

The specimen figured (Fig. 45) is a young male approaching maturity; the third molar is not yet erupted but the details of the teeth are very clearly shown. The species is rather specialized and illustrates to what extent Gibbons have deviated from the central primitive type represented by *Propliopithecus*.

The diet of the Gibbon is essentially omnivorous although with a large preponderance of roots, shoots and fruits: indeed some species live almost entirely upon herbivorous food.

The mandible is not powerful and on the skull the weakness of the zygomatic arches is also striking. The muzzle is elongated but the incisors have retained their almost vertical position. The rows of the teeth are nearly parallel and apt to be inturned at their hinder extremities. There is no definite "ape-shelf" and the tongue space between the anterior teeth is not greatly encroached upon by bone. The upper incisors slope forward, the lateral ones being somewhat pointed. The canines are long saber-like teeth and the upper is much longer than the lower. The upper premolars are bicuspid and set rather more

medially than the molars. The first lower premolar in the specimen figured shows a definite sectorial form, much more pronounced than in some other species. Of the molars the second is the largest and the third is very variable in size. The uppers exhibit the typical trigon, an oblique ridge connecting protocone with metacone, and a hypocone the development of which differs according to the species. In all the lower molars



Fig. 45.—Dentition of Gibbon (*Hylobates hoolek?* Harlan; 9.88-1). The Gibbon is a form less specialized than the larger Anthropoids. This example is a young male with the third molar not yet erupted.

in the figure there is a pronounced hypoconulid almost axial in position and in no species is a paraconid present. The hypoconid is large and by its approximation to the metaconid shuts off the protoconid from the entoconid as in *Propliopithecus*.

The Gibbon then is an Anthropoid which, so far as we know, never attained large proportions but, diverging from the ancestral stock, specialized in its elongating muzzle and tooth forms toward a frugivorous adaptation.

Of the large Anthropoids the Orang-outan of Borneo and Sumatra feeds entirely upon the durian, a fruit which possesses a very tough rind whereas the Gorilla and the Chimpanzee of tropical Africa still have an omnivorous diet consisting of berries, fruit, roots, small mammals, birds and eggs. It will therefore be simpler to consider the African Anthropoids first.

The Gorilla (Fig. 46) is an animal heavier and bulkier than Man and possesses long jaws which give it a superficial resem-



Fig. 46.—Dentition of Gorilla (*Gorilla gorilla*, Wyman; 9.88-14). This is a nearly adult female. Note the clear-cut "crystalline" cusps on the molars. The third molar is not yet fully erupted.

blance to the Baboon. The female is much smaller than the male. The elongation of the muzzle and the large size of the canines cause the limbs of the dental arches to be divergent backwards in the male; they remain approximately parallel in the female. The body of the mandible, though stout, is relatively less deep than in Man. The symphyseal region which may be almost vertical in the female slopes downward and

backward in the male. The "ape-shelf" can be clearly seen jutting backward from the symphysis and the anterior part of the tongue space is encroached upon by bone. The palate, as in other Anthropoids extends behind the last molar tooth.

The lower incisors are almost vertical but those of the upper jaw slope forward. The canines are much larger in the male, the upper being a little longer than the lower. The upper premolars are bicuspid and in the male set rather within the line of the molars. The lower first premolar is sectorial but not markedly so; the second is molariform. Of the lower molars the second is the largest, the third may or may not be smaller than the first. In the upper molars there is a typical trigon with the oblique ridge connecting protocone and metacone but there is also a well-marked hypocone which tends to be somewhat smaller in the third molar than in the others. In the lower molars the hypoconid is rather small but still by its approximation to the large metaconid separates the other two main cusps. The hypoconulid is present on all the molars and is placed well towards the lateral side.

The Chimpanzee (Fig. 47), an Anthropoid about as heavy as Man, is in many respects more man-like than the Gorilla and the teeth have developed certain secondary features also found in our own dentition. The jaws are very similar to those of the Gorilla. The mandible is strong with a moderately deep body. A symphysial region and "ape-shelf" occur as in Gorilla. The tooth rows are almost parallel in the female but diverge forward in the male.

The lower incisors are nearly vertical and the uppers gently sloping. The canines are large and project somewhat laterally as in Gorilla. The upper premolars are bicuspid and set a little within the line of the molars; the lower first is sectorial in appearance and the second molariform. In the molars the cusps are more nipple-shaped than in Gorilla and the crowns show numerous variously arranged tiny grooves or crenations obscuring to some extent the original cuspidation. This crena-

tion also occurs upon the premolars. The first molar, especially in the upper jaw, is often a little larger than the second, a condition also occurring in Man. The third is variable in size and pattern but tends to be smaller than the others. In the mandible the first molar does not present the marked contrast in size with the second premolar so plainly apparent in Man. The upper molars show a typical trigon with an oblique ridge

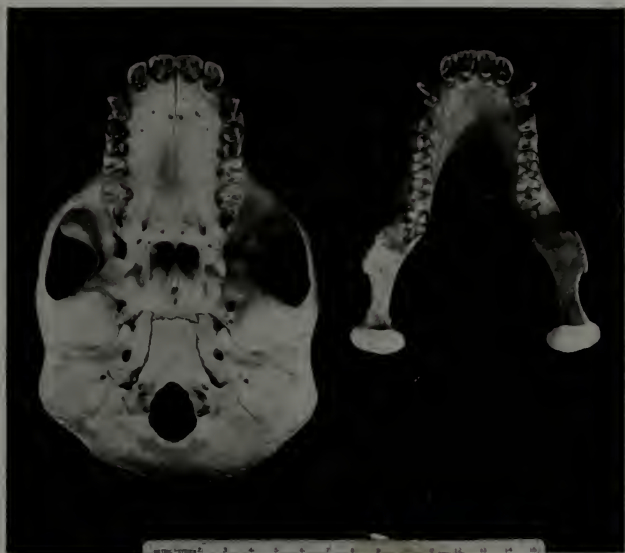


Fig. 47.—Dentition of Chimpanzee (*Pan* sp., 9.88-16). A nearly adult female. Note the slight development of crenations on the molars. The third molar is not yet erupted.

and a hypocone. In the last tooth however either the hypocone or the metacone may be vestigial; or the tooth itself may not erupt. The lower molars exhibit an antero-posterior diameter longer than the transverse and the corners of the crown are not so rounded as in Man. The hypoconid varies greatly. It may be relatively larger than in Gorilla or it may be very small and the entoconid increased in size so that the four principal cusps meet in the center of the crown somewhat as they

do in Man. A hypoconulid may be present on all the teeth and lies rather toward the lateral side.

The Orang (Fig. 48), a pure fruit-feeder, shows a dentition more completely adapted to fruit diet than either of the other great Anthropoids. It is a heavier animal than Man though less bulky than the Gorilla. The muzzle is relatively longer than that of the Chimpanzee and in this respect resembles the Gorilla. As in Gorilla also the palate is prolonged backward some distance



Fig. 48.—Dentition of Orang-utan (*Pongo pygmaeus*, Hoppius; 9.88.5). An adult male. Example of a pure frugivorous dentition in an Anthropoid. Note how crenations obscure the molar pattern.

beyond the last molar. In the male the limbs of the dental arch diverge forward in consequence of the large canines. The body of the mandible is very deep owing to the extreme length of the roots of the teeth. The sloping symphyseal region and the "ape-shelf" are similar to those of the Gorilla.

The lower incisors are practically vertical, the uppers oblique. Of the large laterally projecting canines the upper is the longer. Both premolars and molars exhibit very well the

crenations already noted in less pronounced form in the Chimpanzee. The upper premolars are bicuspid teeth; the first lower shows a more pronounced sectorial character than in any other Anthropoid since it is tilted backward and the enamel clothes the upper part of the anterior root; the second lower premolar may be quite molariform in appearance. In the molar series the second is the largest and the third, especially in the mandible, tends to be of considerable size. The cusps are so low as to be almost indistinguishable in many cases. In the upper molars the trigon, the oblique ridge and the hypocone can all be made out except in the last in which crenations make the outlines very obscure. In the lower molars which are elongated though not so markedly as in the Gorilla the approximation of hypoconid and metaconid causes separation of the two other principal cusps. The hypoconulid present on all the teeth lies axially or to the outer side.

Having now discussed in detail the dentitions of the various Anthropoid Apes so far as the jaws and crowns of the teeth are concerned it will be advantageous to recapitulate several important features before passing on to the teeth of Man. Discussion of the roots of the Anthropoid teeth and of the milk dentition will be taken up in later chapters.

The mandible has a broad ramus and a body only moderately deep, the height of which shows more or less sudden increases in the premolar region and between the lateral incisor and canine. The symphyseal region slopes backward especially in the male and an "ape-shelf" is present in varying degree except in certain Gibbons. The palate extends well back of the last molars especially in some Gibbons and in the male Gorilla and Orang. In all the muzzle is elongated.

The incisors are set in an arch between large and powerful canines beyond which the cheek teeth are arranged in rows almost parallel in the Gibbons and the females of the large Anthropoids but diverging forward in the male Chimpanzee, Gorilla and Orang. The antero-posterior axes of the molars of both jaws are in the same straight line or form an angle

open laterally. Inturning of the hinder ends of the dental arches is seen only in some individuals.

The sloping upper and almost vertical lower incisors meet edge to edge and the upper lateral tends to be pointed. The canines, apart from the sexual difference, are long, except in some Gibbons and are laterally directed. The upper premolars, bicuspid in appearance, are usually set rather within the line of the other cheek teeth; the first lower is sectorial especially in some Gibbons and in the Orang; the second lower is large and molariform, in the Orang more than in other Anthropoids. Premolars and molars alike show crenations which are so marked in the Orang as to obscure the cusp patterns; they are not found in the Gibbons or Gorilla. The molars exhibit many individual variations but in general the following are characteristic. In the Gorilla the cusps are high and triangular, in the Chimpanzee nipple-shaped, in the Orang flat and little marked, in the Gibbon high and rounded. The crowns are rhomboidal above, elongated below except in the Gibbons, and form areas of contact of considerable extent between the successive teeth. In the upper molars the hypocone is very well marked except in the Orang and the oblique ridge is distinct. These features may not be seen so clearly in the third molar which varies greatly in size. In both second and third molars there is a tendency toward reduction of the metacone and hypocone. The second molar is usually the largest. In the lower molars there is sometimes a vestige of the paraconid shear in the Gorilla alone. In the dentition of this animal the metaconid lies a little more posterior to the protoconid than in other Anthropoids. The distance between the metaconid and the entoconid is considerable and a deep cleft occurs on the lateral border of the crown between protoconid and hypoconid. The last-mentioned cusp varies considerably in size but may be quite small and in any case does not project laterally beyond the protoconid. Its base adjoins that of the large metaconid and this connection separates the two other principal cusps. The groove which reaches the inner border

of the tooth between metaconid and entoconid usually passes in a straight obliquely placed line between the hypoconid and the hypoconulid which is present on all the teeth and tends to lie rather toward the lateral aspect. Balancing the hypoconulid there is sometimes developed from the cingulum a cusp behind the entoconid at the postero-mesial corner of the tooth. The hypoconulid tends to be small most frequently in the Chimpanzee.

CHAPTER VII

THE HUMAN DENTITION

Earliest known human type—The Heidelberg mandible—European Races during the Pleistocene—*Homo aurignacensis*—Neandertal Man—Relation of the Neandertal Race to modern Man—The teeth of Neandertal Man—Modern Races—The Tasmanian—The European dentition—Relative position of the Negro—Effects of civilization upon White and Negro Races—Parallelism in the evolution of Primates.

GLACIAL OR PALEOLITHIC MAN

In dealing with other families of Primates we have endeavored to trace the line of evolution progressively from some early or primitive form. In the case of Man we are unable to do this in a manner altogether satisfactory, since no human or directly pre-human type has yet been discovered which can with certainty be assigned to a period more remote than the early Glacial epoch.

All the evidence presented by Man's body indicates his origin in a cursorial, predatory type of Anthropoid which left the trees at a comparatively early period in its evolution and hence escaped the specializations exhibited by modern omnivorous and frugivorous Anthropoids but, on the other hand, became adapted as a ground living animal, retaining the omnivorous habit and using its fore-limbs in the manufacture of simple tools and instruments of assistance in obtaining and preparing food.

The earliest authentic example of the human race, namely, Heidelberg Man (Fig. 49), is known only from the mandible recovered from the valley of the Neckar about six miles from Heidelberg. Although typically human this mandible presents

certain quite primitive and generalized features. Whether the individual existed during the first or the second interglacial phase is disputed. But from mammalian remains in the same and in contemporaneous deposits we infer that the country in which he lived was well forested and possessed a relatively moist climate.

The mandible is extraordinarily massive and although it is considerably longer than any mandible of today it is not really much longer in the dental arch than many modern jaws. The unusual length is due to the marked breadth of the ramus.



Fig. 42.—Occlusal view of the Heidelberg mandible (F. 3, W.R.U.; from cast by Krantz). This cast has been broken at the symphysis and in the right ramus. Note the cruciform pattern of furrows on the molar teeth and the angle between the long axes of the first and second molars, both features distinctively human.

In the great vertical depth of the body, the breadth of the ramus, the form of the symphysial region, the absence of an "ape-shelf" and the occurrence of merely a moderate amount of bony tissue encroaching upon the anterior part of the tongue space, the Heidelberg mandible displays ancestral features reminiscent of *Propliopithecus*. The masseter and internal pterygoid must have been the most powerful masticatory muscles; the area for attachment of the temporal indicates that it was not disproportionately large for the massive skull. Similar features are to be noted in *Propliopithecus*. The

mylohyoid ridge is less clearly marked than in either modern or Neandertal Man, also a primitive feature.

The teeth, though retaining many ancestral features, are typically human in form and no larger than those to be found in many modern Australian skulls.

The incisors are vertical and must have met the corresponding upper teeth in an edge to edge bite. The canines, like those of *Propliopithecus*, are stout but can have projected little or not at all beyond the incisors. The second premolar is larger than the first and more definitely bicuspid as it is in *Propliopithecus* and the first shows none of the specialization exhibited in the corresponding tooth of the recent Anthropoids. Both premolars are relatively large and their labial surface projects beyond the lateral border of the molar arch. Incisors, canines and premolars in Heidelberg Man may be said to be arranged in an oval curve, whereas those of modern Man are set rather in parabolic form.

The molars are stout but present the primitive relationship of subequal size in the first and second; the third is somewhat reduced. All the molars exhibit a hypoconulid and are relatively less transversely widened than many modern molars.

Distinctively human features are obvious throughout the dentition, some of which being primitive have already been described. The vertical incisors with edge to edge bite, the stump-like canines, the proportions of the premolars are all definitely features of the human dentition. But it is in the pattern and arrangement of the molars that the human character is most strikingly seen.

The maximum diameters of the crown in the molars are considerably greater than those of the occlusal surface. The protoconid and more especially the metaconid are much reduced in size whereas the hypoconid is relatively large and the entoconid greatly exaggerated. All these cusps are slightly curtailed, however, by the rounding off of the corners of the crown, a feature which tends to reduce the area of contact between successive teeth. The transverse and antero-posterior

diameters of the crown are much more nearly alike than in Anthropoids and as a result of this the two inner cusps are drawn more closely together while the furrow between the labial surfaces of protoconid and hypoconid is very slightly marked. As a result of the altered relationships of the cusps the furrows upon the occlusal surface, instead of presenting an appearance similar to that of the molars in Gorilla, are arranged in cruciform pattern. The very small metaconid does not come into contact at all with the hypoconid and the well-developed entoconid encroaches upon the area of the crown occupied in the Anthropoids by the metaconid, so that all four principal cusps meet at the central point of the occlusal surface. The groove between metaconid and entoconid is continuous in a transverse line with that separating the protoconid from the hypoconid, whereas in Anthropoids it is continuous obliquely backward with the furrow between the hypoconid and the hypoconulid. Another consequence of the relatively large cusps on the talonid is the increase in transverse breadth of the posterior moiety of the tooth over the anterior part. The hypoconulid is not displaced so far laterally as in Anthropoids. In addition to the foregoing facts relating to the appearance of the individual teeth themselves, essentially human characters are found in the general arrangement of the cheek teeth in the jaw. Instead of the premolars and molars forming either a straight line antero-posteriorly or an arch very slightly concave laterally, they are set in a curve most pronounced anteriorly indeed but concave throughout towards the tongue. The antero-posterior axis of the first molar is set at an angle with that of the second, a feature which is distinctively human though more pronounced in some mandibles than in others.

The conspicuous even wearing of all the teeth causes them to resemble those of more recent Man in whom the teeth are worn by the mastication of food prepared from cereals ground between gritty mill-stones and suggests that Heidelberg Man was already in the habit of masticating cakes prepared from

crude flour. This seems further to be borne out by the flattened condyles; but the condyles are subject to great variation in the human race and in the appearance of them too great confidence should not be placed.

Special features, wherein Heidelberg Man differs not only from more ancestral Primate types and from Anthropoids but indeed from modern Man and his late Pleistocene forerunners, are the stoutness of the teeth in which the crown and root merge without the occurrence of any narrowed intermediate portion or neck and in tendency to fusion of the roots, a condition called by Keith, *taurodontism* (see page 146). In the stoutness of the teeth Heidelberg Man is resembled by another individual, the skull of which, also very primitive, was recovered from the limestone breccia of Forbes Quarry, Gibraltar.

The Gibraltar skull, pronounced by some to be that of a woman, probably belonged to a Neandertaloid individual, the most striking feature being the short and relatively wide palate. Its exact relationship to the other fossil human skulls is uncertain; we know that during the Glacial period there were several different types of skull.

Recent discoveries have shown that there were in Europe two distinct races of men during the later part of the Great Ice age. One of these was similar and very probably ancestral to ourselves; the other, the Neandertal race, shorter and bulkier, large jawed and beetle browed with slouching gait and stooping shoulders, was named after the site of discovery of the first recognized cranial fragments. Of these two human forms the Neandertal race probably originated from the type described as Heidelberg Man and although this is not positive it may be that the other form, our ancestor, *Homo aurignacensis* had also the same origin. But *H. aurignacensis* appears quite suddenly in the geological horizon of the later Pleistocene. It becomes necessary then to compare examples of Neandertal and Aurignacian Man. For this purpose we shall examine the jaws of a young Neandertal boy of about fourteen years of age

known as *H. mousteriensis hauseri* on the one hand and on the other a cranium dating also from the later part of the Pleistocene and belonging to the Aurignacian type. Both specimens were discovered in the South of France.

In most respects *H. aurignacensis* (Fig. 50) presents very modern characteristics. The mandible, though powerful, has a well-marked chin and the vertical depth of the body is considerably greater near the symphysis than in the molar



Fig. 50.—Occlusal view of dentition in *Homo aurignacensis hauseri* (F. 2, W.R.U.; from cast by Krantz). This represents our own Pleistocene forerunner.

region. The tongue space is well excavated. The palate is rather long and narrow. Indeed the limbs of the dental arches though shorter than those of Heidelberg Man are still almost parallel. To a certain extent this is due to the long narrow skull. Among modern races, generally speaking, the long headed more closely resemble *H. aurignacensis* in the form of the dental arch than do the broad short headed people.

The teeth themselves are smaller and less stout than in Heidelberg Man and possess a constricted neck at the gum

line. The small lower incisors are vertical. The uppers are also vertical, the small size of the lateral members resulting in the stout but non-projecting upper canines being placed relatively close together. The lower canines again are also stout teeth. The upper premolars are bicuspid and set well within the molar line, the second being distinctly the smaller. In the lower premolars this relation is reversed but though the second is the larger of the two it is nevertheless much smaller than the first molar. As in the case of the upper teeth the labial face of the lower molars does not project so far laterally as the labial aspect of the molars. In both jaws the first molar is the largest and most reminiscent of ancestral form and the size diminishes through the second to the third. The upper molars are rhomboidal and in each the transverse diameter of the crown measured over the protocone and the paracone considerably exceeds the antero-posterior dimensions. The first shows a well-developed hypocone, the second a hypocone obviously reduced and the third practically no hypocone at all; in this last tooth the metacone also is considerably reduced. In the lower molar series as in the upper the first tooth is the most stable, the more progressive second and third are smaller than the first. Each molar displays the hypoconulid (except the right third) a cusp which tends to be absent in modern Man especially on the second molar. All the lower molars are remarkable for their rounded contour. The antero-posterior axis of the first is set at an angle with that of the second in characteristically human fashion. As in *H. heidelbergensis* the teeth are considerably worn down.

Turning now to the Neandertal type (*Homo mousteriensis* hauseri, Fig. 51) we find the teeth in general somewhat similar to, though larger than those of *H. aurignacensis* but also distinctly human. The mandible has a more rounded angle than that of *H. aurignacensis* and a body of less vertical depth especially in the incisor area. The mental region is very differently shaped, there being no chin. A much greater deposit of bone eneroaches upon the tongue area than in *H.*

aurignacensis but not so marked as in Heidelberg Man. The limbs of the dental arches are divergent owing to the considerable basiscranial breadth and the arches themselves are squarer. All the teeth show a well-marked neck at the gingival line and the roots are long and unfused. All the incisors are stout, relatively large and long rooted teeth and the crowns are vertically placed. The upper teeth overlap the lower very slightly. The spatulate form of the upper median incisors is



Fig. 51.—Occlusal view of dentition in Neandertal Man (*Homo mousteriensis* hauseri, F.I, W.R.U.; from cast by Krantz). A specialized and aberrant form of Man appearing and disappearing suddenly in Europe during the Pleistocene Period. The left mandibular milk canine is retained in this skull.

very pronounced and in these as well as in the laterals the long axis of the root forms an angle with that of the crown, a secondary specialization also found in the great modern Anthropoids. The cingulum is elevated into a small palatal cusp more pronounced in the lateral than in the central upper incisor. The canines are stout teeth projecting only slightly beyond the general occlusal plane. The maxillary canines possess a very pronounced palatal cingular cusp connected

with the apex of the crown by a low ridge. The upper premolars have quite massive crowns and are subequal in size. In the mandible the premolars present a rounded and obliquely sloping labial surface. Their main cusp lies in the vertical axis of the tooth and in consequence the occlusal surface is directed obliquely inwards. The second premolar is especially massive and molariform through the development of a posterior moiety. The molars again are powerful teeth with long almost parallel and unfused roots; the third is not yet fully erupted. Both first and second maxillary molars present a typical trigon with an oblique ridge and in addition a well-developed hypocone. They are subequal in size with the antero-posterior dimension almost equal to the transverse. The third molar crown, smaller in size, does not show the cusps so clearly as the more anterior teeth but it also possesses a hypocone. The teeth are obliquely rhomboidal and except in the third molar the corners are but slightly rounded off. The lower molars are typically human in the cruciform arrangement of their furrows. Each possesses a hypoconulid but displays advanced characters in certain respects. The transverse ridge between protoconid and metaconid is quite pronounced. The occlusal surface is narrower than the crown itself. The hypoconulid tends to be subdivided. In addition to these advanced features of individual teeth the purely human character of an angle between the antero-posterior axis of the first lower molar and that of the second is present. All the teeth are well rounded and are subequal in antero-posterior length. An interesting feature reminiscent of the Eocene Primates and found also as a small tubercle in the Gorilla molar is a small sixth cusp between the metaconid and the entoconid.

Having drawn attention to the main distinctive marks of the Aurignacian and Neandertal dentitions it may be asked if the latter shows in reality any features not to be observed in some at least of modern crania. There is no doubt that every feature discussed can also be found in any fair-sized collection of recent skulls although perhaps the extent and blending of the

features will not be the same. It might seem, therefore, that the Neandertal type is really ancestral to our own race as indeed has been and is the view of many anatomists; that all human races have passed at some period or other of their history through a Neandertal stage. This is a question difficult to settle in any case and quite impossible if we consider only the teeth. Stress has been laid upon the fact that there seems to be an unusually large number of specialized features, many of them present to a pronounced degree, in the dentition of Neandertal Man. More than this we know that he could not be the direct ancestor at least of Aurignacian Man since both lived in the same period. The features in which the Neandertal dentition differs from that of *H. aurignacensis* or of modern Man are largely secondary specializations many of which are present also in Anthropoids as the result of parallel evolution. These indicate the specialized and aberrant condition of Neandertal Man so strongly confirmed by the characters of other parts of the skeleton. It is true that there were many variations in Neandertal Man as there are in modern Europeans, which variations affect not alone the skull and skeleton but also the teeth, and hence the dentition of the example described stands no more typical of all than a single example would represent every variety in the dentition of modern Europeans. Indeed so pronounced and aberrant are certain features exhibited by some Neandertal teeth that we must briefly consider these peculiarities.

Examination by the radiographic method of the mandible of a great Anthropoid or a modern human being shows the roots of the teeth varying somewhat in length, in disposition and in relation to the inferior dental canal. In the majority of cases one feature is apparent in all, namely, that the pulp chamber, though small, is well defined and lies entirely or almost entirely outside the limit of the alveolar process of the jaw. In the Heidelberg mandible the pulp chamber is less sharply outlined and although its limits do not greatly extend below the free alveolar border still the pulp chamber is large and its

borders overrun the limit usual in modern Man. For such stout teeth possessing no obvious neck the roots strike one as rather short. The "woolly" appearance presented by the border of the pulp chamber is due to the formation of secondary dentine normally laid down in all teeth as the wear increases and especially after the enamel coated surface of the cusps is lost. A similar shortening of the roots with increase in size of the pulp cavity occurs in the molar teeth of the very specialized Daubentonina as compared with the less specialized Indrisinae. It is worthy of record that we meet these characters greatly exaggerated in some but by no means in all of the Neandertal race. In some molars from Krapina and in those from St. Brelade's Bay, Jersey (Fig. 98), the shortness of the roots which are fused into a single mass and the large size of the pulp chamber partially encroached upon by secondary dentine are strikingly seen. In the case of the Jersey teeth the jaws are unknown but in fragments of Krapina skulls the lowering of the margin of the pulp chamber below the alveolar border is quite pronounced. It is impossible to disregard these features which are certainly not primitive but exceedingly specialized and though they may be met with even in modern Man the extent to which they occur is much less than in the Krapina Neandertalers. The short fused roots, large pulp cavity and absence of a neck give a general appearance simulating the teeth of the ox and Keith has, therefore, proposed for this variety the adjective *taurodont* in distinction from the more dog-like or *cynodont* roots of the usual form.

Having now discussed the two main types of Glacial Man and having indicated that *H. aurignacensis* is probably our ancestral representative, whereas Neandertal Man is an aberrant and specialized form which probably was ousted by his less specialized competitor, we may turn to the consideration of modern human races.

MODERN MAN

All human races of today are obviously different from Heidelberg Man in possessing greater tongue space and smaller jaws though not necessarily smaller teeth. They are unlike Neandertal Man in the possession of a chin. Their features recall those of *H. aurignacensis*, a long-headed European of the Glacial period.

It is an interesting fact that the long-headed or dolicocephalic type of Man has always been pre-eminent as a sea rover and we shall take as our first example the skull of a native Tasmanian (Fig. 52), a type who could only have attained his final distribution after considerable travel, as representing the most primitive modern race though recently become extinct. Unfortunately the dentition is not very complete and no features of the incisor and canine teeth can be directly noted. These teeth do not greatly differ however from the corresponding teeth of other human races and therefore we shall not pause over these or indeed over the premolars which resemble those of *H. aurignacensis* rather than of Neandertal Man. It is the molars to which attention is drawn at the moment. All have well-marked necks, parallel unfused roots and large crowns. The total length of grinding surface of the three mandibular molars is as great as in Heidelberg Man or in *H. mousteriensis*. It is considerably greater than in *H. aurignacensis*. The first molar is actually longer than that of Heidelberg Man but the second is shorter. In the maxilla we find likewise that the total molar surface is longer than in *H. aurignacensis* but is slightly shorter than that of the Neandertaler. The first maxillary molar is again the largest. This increase in size, usually relative but in certain instances actual, is characteristic of modern Man. Typically human features such as the angle between the axes of the first and second mandibular molars need not be dwelt upon since they have already been emphasized in the descriptions of fossil Man. When we look at the individual teeth we note several features which

may be rightly inferred to have appeared comparatively recently in Man's history. For example the second upper molar has lost its hypocone as an independent cusp while its metacone is much reduced by the rounding of its contour. These features are still more marked in the third molar. In the lower molars, especially the second, the posterior moiety representing the talonid has increased considerably in transverse breadth

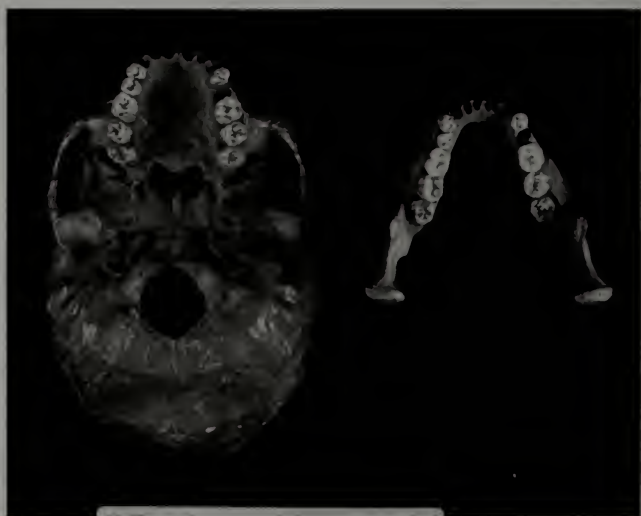


Fig. 52.—Occlusal view of dentition in a native Tasmanian woman (O.102, W.R.U.). A primitive modern race recently become extinct.

so that it now may actually exceed that of the anterior part. The large size of the human hypoconid and entoconid is well illustrated by this example. Many features however are primitive: the molars are large and more especially they are relatively long: each lower molar possesses a hypoconulid which is axial in position: the distance between the tips of the metaconid and the entoconid is relatively great, in the first molar greater than in the others: the lateral groove marking off the protoconid from the hypoconid is quite extensive. In spite of the presence of a well-developed chin the body of the mandible

is strikingly shallow and in this respect recalls the mandible of the Neandertaler. When the foregoing facts are carefully weighed there is no doubt that Tasmanian Man is a primitive modern race.

Next let us consider the general dental features of present day Europeans. Again, as in Neandertal Man, we find long and short headed varieties. In the latter the limbs of the dental arches tend to be more divergent and the arches themselves shorter in antero-posterior length. We cannot consider further differences here.

As an example of the modern European dentition* we have chosen a skull (Fig. 53) in which the dental arch is rather long and its limbs not very divergent. In their occlusion the upper incisors only just overlap the small lower teeth and the small size of the upper molars and the marked reduction in the second lower molar result in the practical elimination of alternate occlusion in the molar region. These two features are worth noting. If we refer for a moment to *H. aurignacensis*, we shall find that in addition to edge to edge bite of the incisors the molars alternate so that although the majority of the crown of each upper molar occludes with the corresponding lower yet nearly one-third of the crown is in occlusion with the lower molar next behind. The same is true of the Tasmanian skull. In Anglo-Saxon times almost the entire population possessed an edge to edge incisor bite. After the lapse of less than a thousand years ninety-five per cent of

*In order to correlate the zoological cusp terminology used in this book with the terms commonly used by dentists the following table (Osborn: *Evolution of Mammalian Molar Teeth*, 1907) is presented:

Upper Molars

Anterior palatal	Protocone	} Primitive triangle, or trigon.
Anterior buccal	Paracone	
Posterior buccal	Metacone	
Posterior palatal	Hypocone	Primitive heel, or talon.

Lower Molars

Anterior buccal	Protoconid	} Primitive triangle, or trigonid.
Anterior lingual	Metaconid	
Posterior buccal	Hypoconid	} Primitive heel, or talonid.
Posterior lingual	Entoconid	
Posterior mesial	Hypoconulid	

modern Englishmen, as Keith points out, possess upper incisors which overlap the lower teeth. Hence in the development of modern Europeans certain changes of quite marked extent have occurred even in recent times. A prominent chin and capacious tongue space are present in this as in all modern human skulls.

The canines are prominent, stump-like, non-projecting teeth which do not stand out from the almost uniform contour of the



Fig. 53.—Occlusal view of dentition of modern European (Skull 248, W.R.U.). Effect of civilization upon a dentition like that presented in Fig. 51.

antemolar dental arch. The premolars are small and set rather within the line of the molar teeth. The second premolar, having its posterior moiety very slightly developed, appears small beside the large and stable first molar. Of the molars the first is the largest and the progressive reduction in size from before backwards is well seen. The angle between the antero-posterior axes of the first and second upper molars is quite apparent but in the mandible the eruption of the corresponding teeth is less regular. In all three upper molars the metacone is reduced:

in the first there is a fair-sized hypocone but this cusp is reduced in the second and absent in the third. A hypoconulid occurs in the first and third mandibular molars but is absent from the second. All these teeth exhibit a greater transverse breadth of the posterior moiety (taloid), are well-rounded in contour and show the typically human cruciform arrangement of furrows. The hypoconulid of the first molar is almost in the axial line but in the more progressive third which possesses a strikingly large entoconid and a correspondingly small hypoconid this cusp lies more on the lateral side.

It is true that there are marked changes going on in the jaws of modern Europeans. It is true also that there is great variation in the size and development of the third molar but it must be remembered that this tooth is normally small in the ancestors of modern human stock and therefore increase in its size is much more noteworthy than reduction. The second molar is undergoing most obvious retrogression in the human race, especially in the Europeans. We see this clearly in its reduction in size and its loss of cusps but it will be still more evident when we have discussed the anomalies of the human dentition.

The only other human type which we shall consider in this account is the Negro. Frequently in every-day talk we include the Negro among "lower races" of Mankind although there seems to be no other justification for this than the assumption that White Man is the most highly evolved human type. If we pause to consider what we really mean by the indefinite term "highly evolved" we shall readily discover that there is at least doubt concerning the validity of our standard. If we mean that White Man is more adaptable than the Negro, we merely infer that the former has retained to a greater degree the primitive potentiality of adequate response to environmental conditions and since the Negro is less adaptable he must be more specialized. But specialization may also be understood by the term "highly evolved." The physical characters of the Negro show indeed that he is an advanced special-

ized form, considerably more specialized indeed than the European. The Bushmen and the Pygmies of the Congo forests are more primitive and specialized than other Negro races. In this account we shall examine simply the dentition of the American Negro although he is not typical of the true African race since the changes which we have already noted as occurring in quite recent times in Europeans are to be found in him also.

The skull of which Fig. 54 is a photograph is unusually



Fig. 54.—Occlusal view of dentition of American Negro (Skull 524, W.R.U.). In some respects a very specialized dentition modified in recent centuries by civilization.

broad and therefore the length of the dental arch is somewhat obscured by the divergence of the molar series. The general setting of the teeth in the jaws is very similar to that of the European except that there is greater spacing of the teeth of the upper jaw. The overlapping of the upper incisors and the occlusion of one maxillary molar solely with the corresponding tooth of the mandible occur here as in many Europeans. In the typical African Negro, however, the edge to edge bite of the incisors and the incompletely alternate occlu-

sion of the molars is found as in Tasmanian and in Aurignacian Man. The mandibular body is not strikingly deep and the chin is very prominent. The upper incisors are large teeth and like the lowers have their crowns set vertically. The canines though stout do not project beyond the occlusal surface of the neighboring teeth nor do they break the uniformity of the dental arch. There is nothing particularly noteworthy about the premolars although in some Negroes the second lower premolar possesses a large posterior moiety like that shown by *H. mousteriensis* (Fig. 51). The molars as in the White race present rounded contours. The first maxillary molar is the largest and exhibits a hypocone; the second which is not so large and the still smaller third have not this cusp and in addition show a reduced metacone. In the present case the antero-posterior axes of the upper molars are erratic. In the mandible the first and third molars are subequal, the second is smaller. The axis of the first makes the typical human angle with that of the second. Each presents a hypoconulid which is axial in the first but progressively more laterally placed in the second and third. The last tooth shows its advanced nature not only in its size and in the position of its hypoconulid but also in the great transverse breadth of the posterior moiety of the crown. The complexity of the secondary grooves upon the crowns of the cheek teeth increasing to a maximum in the third molar also demonstrate advanced specialization in the Negro.

We may now summarize the characteristics of the human dentition in the following manner. The Tasmanian, though showing some specialized features, presents a greater number of primitive traits than other modern races. The European in historic times has undergone marked changes in his jaws and dentition and now presents an interesting admixture of primitive features mingled with characters indicating very recent adaptation. The Negro also exhibits marked recent modifications, but possesses a dentition more specialized in certain respects than that of the European.

In looking back over this short review of the Primate dentition in general the reader cannot fail to be impressed, as the author has been, by the striking similarity shown in their evolutionary progress by all families no matter at what stage in ancestral Primate history these families have diverged. Further he will realize how definitely parallel are the lines of evolution in tooth forms presented even by diverse orders of Mammals.

CHAPTER VIII

ANOMALIES OF THE HUMAN DENTITION

Significance of anomalies—Increased number of incisors—Imperfect developmental subdivision of teeth—Para-pre-molars—Variations of the third molar—Accessory molars—Instability of the second and third Molars—Increase of cusps—Paramolars—Retention of deciduous teeth.

In the explanation of variations in number, position and form of the human teeth dental surgeons have before them an interesting and difficult study and it is much to be regretted that the frequency of occurrence of these anomalies does not stimulate to investigation, more than has been the case hitherto, those who are brought constantly into touch with these abnormalities in the course of their daily routine. Too often the valuable data to be obtained only by the dentist are lost or irrevocably destroyed in consequence of the widespread tendency to consider anomalies merely as freaks. Professor Bolk of Amsterdam has recently given much attention to this subject and has published highly original and stimulating views which should encourage more general research along the line of anomalies of teeth. There is no doubt that certain variations are simply sports but the fact that some fall into this category is by no means justification for considering as such all departures from the normal. We are handicapped at present by lack of sufficient information regarding the variations in teeth among other Mammals. That Man is not isolated in this respect is indicated by many scattered published notes of similar anomalies occurring in other families and in many orders of Mammals. In Anthropoids especially deviations from the normal dentition have been recorded but one learns occasionally of abnormali-

ties appearing in other Anthrozoidea and in the Lemurs. The example of *Potamogale* already illustrated (Fig. 33) shows retention of a deciduous tooth. In other Insectivora indeed the apparent mingling of the milk and permanent dentitions has presented many perplexing problems. In every large collection of canine skulls many are to be found in which the last lower molar has never erupted. In this study it will only be possible to consider briefly some variations in the dentition of Man.

Generally speaking anomalies of the human dentition, beyond retention of certain of the milk teeth, are those of variation in position, number and conformation of the permanent set.

With variations in position of normal teeth in either dentition we have nothing to do since these are always of pathological origin so far as is known but it is necessary to review rapidly examples of the other types.

Fig. 55 shows a variation met with perhaps more frequently in the skulls of American aborigines than in those of the White race. An extra tooth occurs between the upper median incisors which seem normally formed in every respect. From the appearance of these teeth it is obvious that the anomalous incisor cannot have occurred as the result of division of a normal incisor, a process known as schizogenesis. With it must be contrasted the split incisor which is occasionally observed. Inasmuch as genuine subdivision may result in the production of an extra tooth between the central and lateral incisors or between the lateral incisor and the canine, it has been stated that our normal upper incisors represent numbers 2 and 4 of a series consisting originally of five teeth such as occurs today in the Opossum. This interpretation however cannot be considered seriously in view of the very different modes of origin of the two types of supernumerary incisors just mentioned. Again it has been suggested that subdivision or diminutive size of the lateral incisor has been brought about by the occurrence at and the splitting by the junction of the premaxillary and maxillary elements of the upper jaw of the rudiment

of this tooth. Since schizogenetic division is met with also in the case of the central incisor it does not seem possible to accept this explanation as altogether satisfactory. The extra tooth figured in Fig. 55 may occur in the normal arch as represented in the present case or upon the palatal aspect of the central incisor; it always assumes a stump-form with a curious and typical crown.

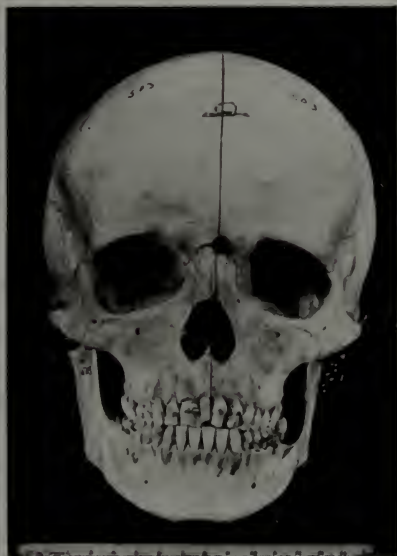


Fig. 55.—Extra median incisor in left upper jaw (European skull 503, W.R.U.)
The median and lateral incisors are of normal size and formation.

Occasionally a condition of imperfect developmental separation of two teeth is met with in either the milk or the permanent dentition (Fig. 56-A) or the germ of the upper lateral incisor may be altogether absent.

Very rarely has apparent duplication of the permanent canine been recorded.

Sometimes small tooth masses have been observed in Man, but more often in Anthropoids on the buccal aspect of the premolars, both between these two teeth and between the second

FIG. 56.—ANOMALIES OF THE HUMAN DENTITION.

- A. Left upper deciduous lateral incisor and canine developmentally fused (from cast by Dr. M. J. Cramer). The corresponding teeth of the right side were normally formed.
- B. Secondary elongation of third lower molar from developmental increase in size of the talonid and deficiency in transverse growth (Colored skull 486, W.R.U.).
- C. Presence of fourth molar (European skull loaned by Mr. B. H. Broadbent.) This tooth which can be seen still embedded in the jaw is of typical molar size and form and occurs only on the left side of the mandible.
- D. Retained upper milk canine and second molar. Deficiency of metacone in second permanent molar (European skull 317, W.R.U.). The permanent canine and second premolar can be seen unerupted below the corresponding deciduous teeth in this man of 35 years. There is deficiency in growth of the alveolar process of the jaw in the vicinity of these teeth. Absence of the metacone is a not infrequent condition in the second maxillary molar.
- E. Stump-like left upper third molar (Colored skull 523, W.R.U.).
- F. Paramolar of the cusp type attached to left upper second molar (Colored skull 416, W.R.U.).
- G. Paramolar of the cusp type attached to lower right third molar (Colored skull 388, W.R.U.).
- H. Carabelli's tubercle on right upper first molar (European skull 392, W.R.U.).
- I. Extra cusp between metaconid and entoconid on right lower first molar (European skull 471, W.R.U.).
- J. Retained right lower second deciduous molar (Colored skull 441, W.R.U.). Note how all the molars are coated with tartar on this side. The left teeth are clean. There is no sign of a second premolar.

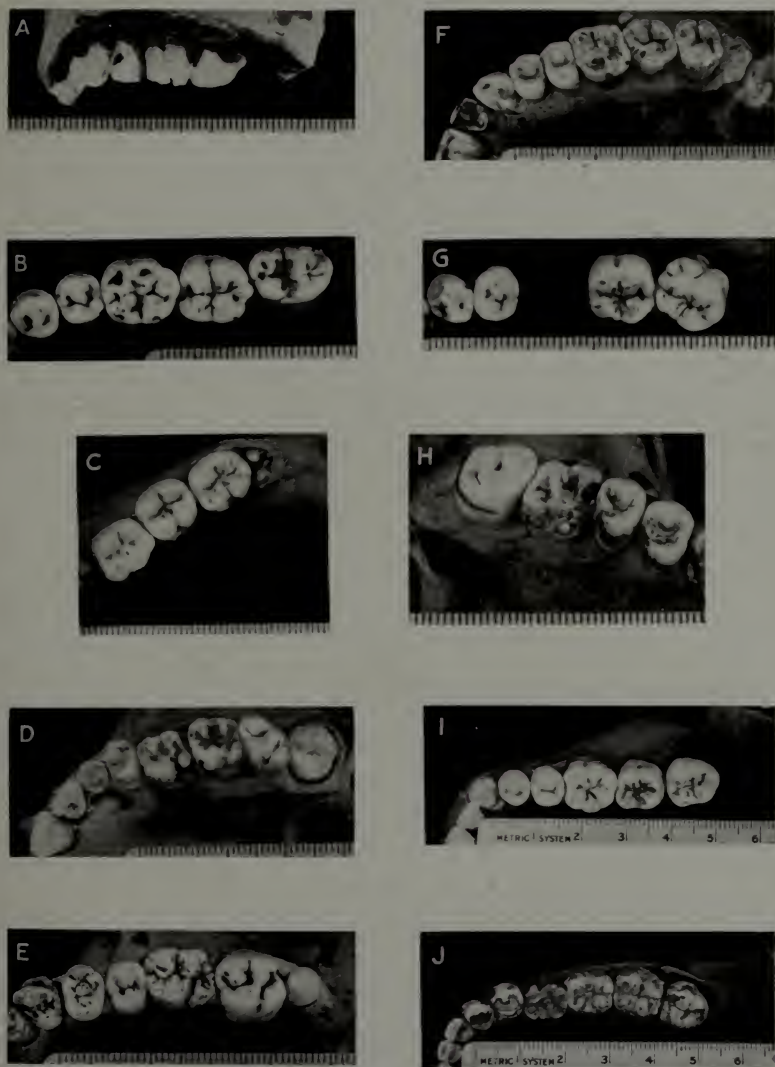


Fig. 56.--Anomalies of the Human Dentition.
(For description, see opposite page.)

premolar and the first molar of the maxilla. Indeed such anomalies as have already been touched upon are much more frequent in the upper than in the lower jaw. It is variation in the molar series which occurs most frequently and has attracted greatest attention.

Anomalies among the molars affect number and appearance. Extra teeth and extra cusps are in some instances indeed intimately related in origin but since this is not always so one must carefully avoid generalizations in discussing anomalies.

The variation in size of the last molar and its not infrequent absence indicate a condition of instability in this region but the fact that the last molar is smaller than the others and is often lacking in the normal molar cusp formation does not in itself indicate degeneration in the modern human dentition. As we have already seen these features occur in fossil Man; they are present also even in primitive Mammals and they seem to result from there being no tooth with which it may occlude behind the third molar.

It has been shown previously that in the specialized Negro race there is a marked tendency to elongation of the last lower molar through exaggerated size of the hypoconulid (Fig. 56-B). The same feature has been noted in the Gorilla and Orang among Anthropoids and in all the most specialized of the Old-World Monkeys. We are also familiar with its occurrence in the purely herbivorous Marsupials and shall meet it again in other orders of Mammals where it is likewise a secondary adaptation.

It is a curious and as yet unexplained fact that, whereas extreme reduction of the last molar is more frequently observed in the maxilla, actual absence of this tooth occurs more often in the mandible. In many people none of the wisdom teeth erupt at all. On the other hand, a fourth molar may be found in either jaw (Fig. 56-C) especially in the Negro and in Melanesian races. It is also observed occasionally in the Gorilla and much more frequently in the Orang in which a fifth tooth has been noted in rare instances. Accessory molars are very infre-

quent in the Gibbon and in the Old-World Monkeys in which latter family their rarity may be connected with the tendency to elongation of the normal third molar. Among American Monkeys *Ateles*, also an advanced form, shows this anomaly most often and again the very specialized genus *Lemur* exhibits it more frequently than the relatively primitive genera of the Lemuroidea. In other orders the anomaly appears constantly in the aberrant canine *Otocyon*, in the very specialized *Armadillos* and toothed Whales, and among Marsupials in the Banded Anteater. It seems, therefore, to be a secondary progression occurring more frequently with increasing specialization until it becomes normal in very aberrant types.*

We have already commented upon the relative instability of the second and third molars in the human dentition. The second upper especially in White races tends to lose its hypocone (see Fig. 54). It may lose its metacone also in which case the not infrequent condition represented in Fig. 56-*D* results. Again both these cusps may be rudimentary or absent in the third upper molar which may be reduced indeed to a simple stump-like tooth (Fig. 56-*E*). Of the lower molars the second loses its hypoconulid more frequently than the third (see Fig. 53) and only the first exhibits this cusp with any regularity.

Regarding the increase in number of cusps of the molars there are several types and the causes underlying these differ in themselves. One not infrequently finds an accessory cusp on the second or third molar fused with the paracone in the upper (Fig. 56-*F*) or with the protoconid in the lower tooth (Fig. 56-*G*). To these we shall return in a moment. There is sometimes a supernumerary cusp on the mesial side of the molar fused with the anterior aspect of the protocone in the upper tooth (Carabelli's tubercle, Fig. 56-*H*), or with the entoconid of the lower. The former of these is stated by some to represent the cingular cusp in the corresponding situation in the upper molar of the

*It is probable that the six successive molars of the Elephant really represent three deciduous and three permanent teeth.

Lemur (Fig. 36) but if this is so the production of the cusp is the result of parallel evolution. According to Bolk the extra cusp occurring on the palatal side of the upper molar and on the lingual side of the lower corresponds to a fourth molar and is genetically different from that on the lateral aspect of the tooth.

In the lower molar the hypoconulid is found subdivided not infrequently, a condition analogous to the splitting of the metacone of the last upper molar seen in the Koala (Fig. 24). Again the lower molars, as in Fig. 56-I, are apt to present a sixth cusp on the lingual side of the crown between the metaconid and the entoconid. This occurs as a small tubercle almost regularly in the Gorilla and is found also in many Eocene Primates (see page 144).

Returning now to the accessory cusp on the lateral aspect of the molars it should be noted that sometimes an extra tooth with a simple crown occurs in the interval between the molars in either the upper or lower jaw and it is impossible to avoid the conclusion that the accessory cusp really represents this supernumerary tooth imperfectly separated off from the normal molar. The extra tooth invariably occurs in the same situation but in the upper jaw, if it be imperfectly separated from the permanent molar, it is represented usually as a cusp whereas in the mandible it most frequently occurs as an accessory root between and lateral to the two normal roots. The presence of this anomaly in its various forms has furnished Bolk with grounds for a theory that the first molar, in which he avers such an abnormality is never found, belongs to the milk dentition along with the supernumerary denticles just described, which may or may not fuse with the second and third molars, and that the second and third successional molars with the occasional fourth belong rightly to the permanent set. Before this view is accepted, however, it must be subjected to further critical examination.

Before terminating this very rapid and by no means complete review of anomalies in the human dentition it is necessary to

pause for a few moments that we may note the retention of milk teeth.

Too commonly current is the impression that some defective eruption of the corresponding successional tooth results from this retention and that if the offending temporary member be extracted the permanent tooth will come normally into place. Retention of certain milk teeth is by no means confined to the human race (see Fig. 33). Indeed among the insectivorous Hedgehogs it is said, though not proved, to be the rule. It occurred occasionally in the Neandertal race (Fig. 51) and is present in some cases of general disease such as rickets.

Any one of the temporary teeth in either jaw may be retained for many years beyond the age at which it is normally lost, perhaps even throughout life (Fig. 56-*D, J*). In many cases a corresponding permanent tooth is present but undergoes mal-eruption. The most significant condition is met with in the case of the second milk molar which is retained perhaps more frequently than any other milk tooth. It may be normally formed even as to the curve of its roots and normally erupted yet the germ of the successional second premolar may be wholly absent without apparent cause. Except after a radiogram has been taken to ascertain the presence and situation of the premolar and the chances of its being induced to come into normal occlusion no sound second milk molar should be extracted.

Sometimes the milk tooth fails to be in proper occlusion after the permanent teeth erupt on each side of it but this is by no means always the case. The retained deciduous tooth may remain healthy and useful throughout life. Its position with regard to the successional set varies somewhat but very frequently its occlusal surface reaches the plane of the occlusal surface of the first permanent molar with which it forms a well marked line of contact. Its longitudinal axis often forms an angle with that of the first molar since it naturally retains the orientation it possessed when occluding with the rest of the milk dentition which is set in an arcade of radius less than that of the permanent dental arch.

CHAPTER IX

THE EDENTATES

RETROGRESSION IN EVOLUTION

Origin and peculiarities of the Edentata—Relation of loss of teeth to skull form—Extinct Armadillos—The zygoma—Experimental results of loss of teeth—Interpretation of changes in the human skull—Old-World Edentates.

The animals included within the order Edentata are undoubtedly modern representatives of stocks differentiating in very remote times from general mammalian ancestors. It is doubtful if all belong in reality to a single order; indeed it is becoming usual to subdivide them in the following manner: the African Aard-varks as possibly related to the very early and primitive Ungulates; the Oriental Pangolins of unknown ancestry; and the American Edentates, the Sloths, Armadillos, and Anteaters, now widely divergent in superficial features but without doubt of common derivation.

The name of the order is itself particularly unfortunate since only the Anteaters and Pangolins are entirely toothless and even in the jaws of these animals vestiges of tooth bands have been discovered. Nevertheless, all members of the order lack median incisors and in this restricted sense they are entitled to the term Edentata.

As regards milk dentition no indication has yet been discovered in the Sloths. On the other hand, temporary teeth have been found in the Aard-vark and in the Armadillos.

In general it may be said that although the teeth of the Edentates vary in number from $\frac{5}{4}$ in the Sloths to as many as 100 in one of the Armadillos they always present certain gen-

eral characters. They are devoid of enamel; their cusps are quickly lost and become replaced by more or less wedge-shaped surfaces, the result of alternate occlusion; they possess permanent pulps and are hypsodont in appearance. These features all indicate the very specialized position of the Edentate dentition.

The American Edentates are well known in Miocene times and there are scattered fragments especially of the Armadillos from yet earlier deposits. Even in the Miocene however the teeth display the same general characters as they do today and the loss of the enamel must therefore be of great antiquity, though even yet a rudiment of the enamel organ persists in the developing teeth. It is quite probable that the American Edentates at least originated from the mammalian stock in Mesozoic times before the differentiation of Insectivora or the ancestors of the Carnivora and of the Ungulata; indeed some go so far as to suggest for them the formation of a special subclass.

A glance at the several skulls (Fig. 57) shows at once that there is not much to be learned in the present study from the teeth themselves but there are marked differences in the skulls, in part the result of the dental condition. Naturally the skull varies considerably in form and proportions according to the character of the food and the manner of feeding but very closely associated with these are the type and even the occurrence of teeth. The Sloths are vegetarians and have a short rounded head with a small face. The Armadillos, largely carrion feeders, possess a flat low skull with a tapering and more or less elongated muzzle. The Anteaters, the diet of which is indicated by their name, exhibit a long narrow almost cylindrical skull, the jaws being long and very slender. In the Sloth the condyle of the mandible lies a short distance above the plane of the teeth; in the Armadillo it may be relatively high; in the Anteater the mandible is very attenuated and delicate and possesses only a vestigial condyle raised but slightly above the mandibular body and the coronoid process is almost non-

existent. In the Santa Cruz deposits of the Miocene of Patagonia however many species of Armadillo were overwhelmed in volcanic ash and these display less uniform characters than the existing representatives. *Stegotherium* for example possessing only few teeth, and these so small that they were no



Fig. 57-A and B.—Lateral aspect of skulls of:
A. Armadillo (*Dasypus sexcinctus*, 9,314-2).
B. Two-toed Sloth (*Choloepus didactylus*, 9,313-2).

more than minute points in the gums, exhibits a facial skeleton and mandible very similar to those of the modern Anteater. On the other hand *Peltephilus*, an Armadillo described by Scott as looking like a tiny Rhinoceros in armor, had a man-

dible the two halves of which were fused together at the symphysis while the condyle was placed at the level of the teeth thus resembling in these respects the Two-toed Sloth.

Comparing the skull of the Armadillo with that of the Sloth or better with that of the Anteater we are impressed by its angularity, by the prominent muscular ridges especially those of the neck muscles hafting the head on to the trunk, by the



Fig. 57-C and D.—Lateral aspects of skulls of:

C. Aard-vark (*Orycteropus capensis*, Oberlin College Collection).

D. Anteater (*Tamandua tetradactyla*, 9.311-1).

Note the slenderness of the mandible in D, and of the edentulous portion in C, the reduction in ruggedness of the skull and the small size of the temporal attachments in the Anteater compared with the skulls of other Edentates.

tapering of the anterior part of the mandibular body and by the slender cylindrical muzzle in front of the first upper teeth. The stout zygoma of the Armadillo attracts attention since the two component parts of this arch do not meet in the Sloth and are even less developed in the Anteater. Variation in form of

the zygoma is not directly connected with the state of the dentition and it must therefore be ignored in our present survey.

In spite of the relative smoothness of the Sloth's skull careful observation shows that although the occiput slopes upward and forward and does not display powerful muscular impressions the masticatory muscles are quite well developed. The area of origin of the bulky temporal muscle is large and rough. The zygomatic arch for the attachment of the masseter, in spite of its incompleteness, is powerfully built and the mandible shows areas also indicative of large temporal and masseter muscles. But turning to the Anteater we find quite a different state of affairs. The mandible is reduced to a mere splinter of bone showing the usual inferior dental and mental foramina since the lower lip must receive its sensory nerves though the teeth be absent, but in spite of a clearly defined angle the condyle is rudimentary and the coronoid a mere vestige. The last named feature suggests a poorly developed temporal muscle and on reference to the skull it is seen that the surface of origin of this muscle is restricted to a tiny postorbital area. The masseteric attachments are relatively less greatly reduced but they are small and the pterygoid attachments almost non-existent. There is a concavity of the palate and weakness in the facial skeleton together with a rounding of the occipital area all clearly indicating the effect of absence of teeth.

The lesson to be learned from the Edentates is then that the absence of teeth results in weakness of the mandible and facial skeleton, greatly reduced size of the masticatory muscles and general smoothness of the skull. We note moreover that these features may be distinguished independently of the type of skull.

Some years ago Professor Anthony in Paris compared the skull of a dog from which six months before he had extracted all the teeth with that of another animal of the same weight from the same litter. The features which we have just ob-

served in the skull of the Anteater Professor Anthony noted in less degree certainly but just as distinctly in the edentulous dog. There were a weak mandible, the rounding of the occiput, the concavity of the palate, the weakness and falling in of the

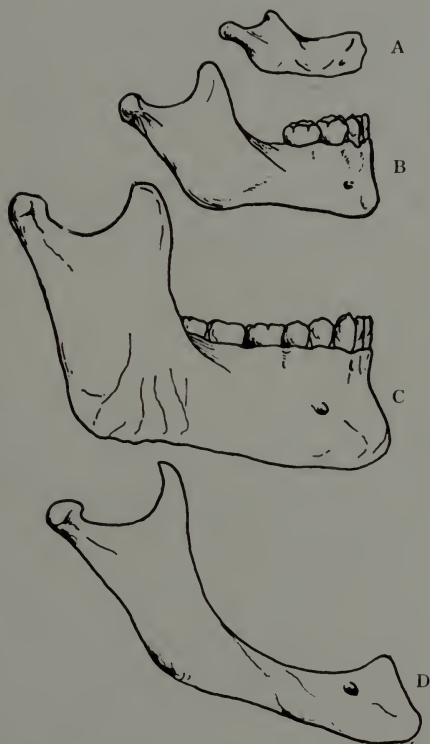


Fig. 58.—The human mandible at different ages (one-half natural size).
 A illustrates the appearance shortly before birth.
 B represents the mandible of a child of four years in whom all the temporary teeth have appeared.
 C shows the mandible of an adult with complete permanent dentition.
 D represents the senile mandible after the loss of all teeth.

zygoma, the small areas of muscular attachment and the smooth and rounded skull.

The features of the old partially or wholly edentulous human being now become explicable. The rounded weak jaw, the ap-

proximation of the nose and chin, the hollowness of the cheeks and temples from wasting of the muscles, the loss of angularity in the skull and the thin tapering neck are apparent in life. Precisely the opposite is noted during adolescence as the milk dentition becomes replaced by the occluding permanent set. Certain local features such as the increase in size of the alveolar portions of the jaws are the direct result of the development of teeth but the permanent dentition must be present in occlusion before the full complement of secondary masticatory

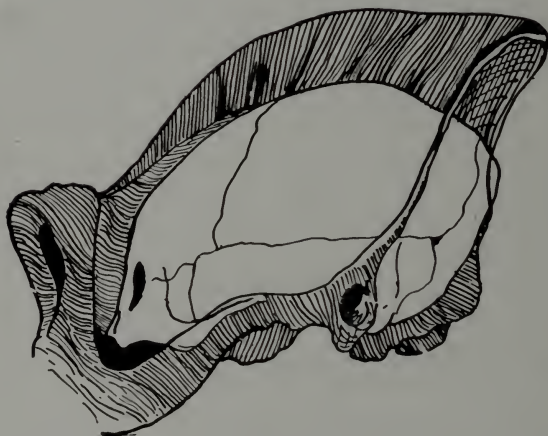


Fig. 59.—Skull of young Gorilla superposed upon that of an adult animal. (After Keith.) Note that with the appearance of the permanent-teeth the temporal and occipital muscles grow so large that additional crests are formed upon the skull for their accommodation and attachment.

features appears. In Fig. 58 we have reproduced the characteristics of the mandible at different periods of life. To render more clearly the changes which the skull undergoes during adolescence reference should be made to Fig. 59 which represents the skull of an infant Gorilla superposed upon that of an adult. This illustration serves to indicate the changes brought about indirectly through the functional use of the teeth.

After this digression we return to the discussion of those

Edentates still remaining, namely the Old-World members of the order.

The skull of the Pangolin recalls at once the general features of the skull of the American Anteater. This curious scaly Oriental Mammal, also an Anteater in habit, is nevertheless widely removed from the American form and the relationship of the two animals is very distant if indeed it exists at all. No teeth are present although vestiges have been found. The features consequent upon absence of teeth occur in the Pangolin as well as in the American Anteater. Thus is presented a case of parallel evolution of which the stimulating factor is known. It is the absence of teeth which has brought about the apparent similarity of the two forms.

It is probable that the Aard-vark (Fig. 57) was originally derived from a mammalian stock possessing the typical placental dental formula:

$$I \frac{3}{3}, C \frac{1}{1}, P \frac{4}{4}, M \frac{3}{3}.$$

but the number of cheek teeth has increased during evolution to $\frac{9}{9}$ although the anterior members of the series like the incisors and canines are quickly lost. The effect of absence of teeth upon the anterior part of the maxilla and mandible is clearly seen. The cheek teeth have the form of double columnus lacking enamel and similar in all general respects to the teeth of the American Edentates but differing in their histological pattern. The milk teeth are brachyodont and each possesses two roots. This curious African Anteater possesses a brain which Elliot Smith states is "distinctly comparable with a primitive Ungulate type" and although there may be some distant relationship, as yet unproven in entirety, with the American Edentates, this speculation is all that we can offer at present regarding its ancestry.

CHAPTER X

THE CARNIVORES

DIVERGENCE IN EVOLUTION

The unity of the order—Ancestral importance of the Dogs—The primitive position of the Civets—The Hyenas—Specialized position of the Cats—Peculiarities of the Weasels—The Raccoons and Bears—Specialized and aberrant features of the Pinnipedia.

The Fissipedia

The order Carnivora today comprises two great suborders: the Fissipedia including the Dogs, Cats, Bears, Raccoons, Civets, Hyenas and Weasels; and the Pinnipedia under which title are ranged the Sea-Lions, the Seals and the Walrus. The ancestry of the Pinnipedia is very imperfectly known and we shall therefore refer to them only in the briefest manner after the other more typical suborder has been considered.

Modern Fissipedia are widely divergent in habit and in physical characters and but for their history as elicited from the rocks it would be realized with difficulty that they have all a common origin. To understand this common origin we must touch upon another suborder of the Carnivora, a group of animals long extinct and known as the Creodonta. The recorded history of the Creodonts began in the Paleocene and they become finally extinct in the Oligocene. They were very varied in character, being carnivorous or omnivorous and some of them very possibly insectivorous in habit. As a rule the dentition was:

$$I \frac{3}{3}, C \frac{1}{1}, P \frac{4}{4}, M \frac{3}{3}, \text{ total } 44.$$

though sometimes a tooth at the premolar-molar junction was lost. The Creodonta, forerunners of the modern Carnivores, were themselves derived from Mesozoic ancestors the characters of which are estimated by Dr. Gregory to have been, among others, the following: 'Small, semi-arboreal, insectivorous and partly carnivorous Placentals with a dental formula:

$$\begin{array}{c} 3. \ 1. \ 4. \ 3 \\ 3. \ 1. \ 4. \ 3, \end{array}$$

a well-developed milk dentition, small tritubercular upper molars, simple premolars, small simple canines, incisors of opposite sides arranged in convergent rather than transverse series. The muzzle was broad and heavy, the skull constricted back of the orbits, the brain-case very small, probably surmounted by a long low sagittal crest, the zygomata not large. Thus the ancestral Carnivores would approach the ancestral Insectivores with which they had common forerunners although they early began to assume predaceous flesh-eating habits, to increase in size and to become adapted for living upon the ground.

Of the Creodonta one family, the Miacidae, small animals none of which attained the size of a fox, is especially significant since its members possessed so many characters in common with the primitive Fissipedia that some authors class them within this suborder. Perhaps one of their most striking features is the constant occurrence of specialization of the last upper premolar and the first lower molar for the purpose of shearing flesh. To these teeth Cuvier long ago gave the name *carnassial*: they are often now called *sectorial* but either term is equally expressive of their function. This specialization of $\frac{P4}{M1}$ is found in the Fissipedia though it is not equally marked in all families.

Of the Fissipedia the Dogs probably represent the central

line of development and this family arose imperceptibly from ancestral Creodonts during the upper Eocene. Almost as old though not so clearly defined in origin the Civets also developed in the upper Eocene. In the Oligocene the Cats appeared with shortening of the skull, increase in the size of certain teeth, and reduction in their number and cusps. At this time also we find the earliest Weasels in which again the skull was shortened. From the Dogs in the lower Miocene originated the Raccoons and in the upper Miocene the Bears, in both cases the teeth increasing in complexity. Lastly the Hyaenas differentiated in the lower Pliocene, probably from the Civets. It is therefore most instructive to take up the consideration of these families with the origin of each in mind. Animals which are solitary rather than gregarious naturally will leave fewer fossilized traces of their existence and hence the history of the Carnivores is not known with the same precision as that of the Ungulates: indeed it is only in the Dogs that the ancestry can be traced back to its inception without a break. In each family progressive features have appeared with change in habits and these have occurred along parallel lines as in other orders. In the chapter on the Primates we have devoted considerable space to the study of parallelism in evolution. We must therefore be content simply to outline the general features of the existing Carnivore families.

First then we take up the Canidae: the Dogs Wolves and Foxes. Of these the Dogs and the Wolves have very similar dentitions although the domesticated Dogs are less purely flesh-eaters than the Wolves: the Fox dentition is easily distinguished. Dogs of the middle Pliocene possess skeletons scarcely distinguishable from those of today and so far back as the middle Miocene the differences are very small. The forerunner of the Canidae in the lower Miocene does not differ greatly from the modern Wolf. But the lower Oligocene ancestor shows so many feline features as to render it probable that here we have the commencing divergence of the Cats from the Dogs.

Fig. 60 illustrates the dentition of the Dog, *Canis familiaris*. The superficial resemblance to the marsupial *Thylacine* (Fig. 20) will be immediately recognized but there is no real similarity and a second glance shows that the teeth differ considerably in the two animals although elongated jaws and the carnivorous adaptation are present in both. Primitive features are seen in the Dog in the low position of the condyle, in the termination of the palate near the hinder upper molar and



Fig. 60.—Dentition of Dog (*Canis familiaris*, 9.7424.43). Note the markedly sectorial last upper premolar and first lower molar, the loss of the last upper and the diminutive size of the last lower molar.

in several dental characters such as the tritubercular formation only slightly modified in the upper molars. The dental formula is:

$$I \frac{3}{3}, C \frac{1}{1}, P \frac{4}{4}, M \frac{2}{3}, \text{total } 42.$$

and thus lacks only one upper molar of the complete placental dentition.

The incisors gradually increase from the first to the third

which is caniniform in the upper jaw. The curved nature of the upper incisor crowns enables their tips to point downward; the lower teeth slope obliquely upward; all have a well-marked cingulum on the inner aspect and tend toward a trefoil design. The canines are long but not so typically carnivorous as in the Cat. The premolars are simple except the last upper tooth and display the primitive increase in size from before backward. The sectorial fourth upper premolar exhibits what corresponds to the metacone-metastyle shear of the Insectivore molar together with a low palatal cusp borne on a separate root; this tooth shears lateral to the sectorial first lower molar. In the maxilla the third molar is non-existent and the second reduced. The first is large and shows the three cusps of the trigon with a well-developed palatal cingulum and a small hypocone. The same features on a much smaller scale distinguish the second molar. The first mandibular molar has a pronounced protoconid-paraconid shear with a diminutive cingular cusp taking the place of the metaconid;* the talonid is low and presents two cusps the hypoconid and the entoconid; its trigonid is thus developed for sectorial purposes. The second molar is small with protoconid and metaconid both low and a basin-shaped talonid: the third is greatly reduced and simplified, even non-existent in many cases.

Passing next to the equally primitive Civets we take as our example the Indian Rasse, *Viverra malaccensis* (Fig. 61) the smallest of the true Civets, an animal which is still arboreal in habit, rapacious, living upon such small animals as it can catch but also probably upon insects as the sharp cusps of its molars indicate. The jaws are elongated, the incisors set more transversely than in the Dog, the condyle is low and the palate extends only a short distance behind the molars. The dental formula of the Rasse is:

*In the Carnivora there is a tendency to lose the metaconid. This is especially obvious in the sectorial first lower molar.

$$I \frac{3}{3}, C \frac{1}{1}, P \frac{4}{4}, M \frac{2}{2}, \text{total } 40.$$

In the specimen figured two left lower incisors and one premolar have been lost during life. The incisors are built upon the same plan as in the Dog and the canines are long, the premolars increase in size from before backward and the fourth lower tooth is molariform. The sectorial fourth upper premolar is also molariform in appearance showing a molar-like trigon with all three cusps and a metacone-metastyle shear. The upper molars remain almost typically tritubercu-



Fig. 61.—Dentition of Indian Rasse (*Viverra malaccensis*, 97422.3). A representative of a family as ancient as the Dogs. The third lower molar is eliminated from this dentition as well as the corresponding upper tooth.

lar but the second is greatly reduced. The sectorial first lower molar has a large trigonid and a low basin-shaped talonid each showing the full complement of three cusps. The second molar is reduced practically to a talonid, the protoconid and paraconid being absent.

There is great variation in the dentition of the Civets (*Viverridae*) according to the food habits (see Fig. 99), the Fossa of Madagascar a purely carnivorous form possessing teeth like

the Cats and the oriental Binturong having teeth with low, mound-like cusps. To this subject of dental variation with food habits in the Carnivora we shall return later (see page 270).

The Hyænas, like the Civets from which they arose, never penetrated to the western hemisphere. They are carrion feeders with the teeth specially modified for the purpose of crushing bones. The rugged strength of the skull is observed at a glance. Large rough areas accommodate the powerful masticatory and neck muscles associated with such stout teeth. Each cheek tooth possesses a pronounced cingulum to protect the soft tissues of the gum against laceration from splinters of crushed bone. The dental formula is:

$$I \frac{3}{3}, C \frac{1}{1}, P \frac{4}{3}, M \frac{1}{1}, \text{total } 34.$$

The sectorial teeth are as usual $\frac{P1}{M4}$ and though there are three varieties of Hyæna these show only minor differences in their dentition. The upper molar is reduced in all but more in the Spotted Hyæna than in the Striped; the lower molar also is more specialized in the Spotted Hyæna, having lost its metaconid and possessing a mere vestige of a talonid. A closely associated animal, the Aard-wolf, also a carrion feeder, exhibits a very degenerate dentition which however need not detain us.

At the beginning of this chapter it was observed that the Cats differentiated in the Oligocene from ancestors common to them and to the Dogs. In the Cats (Felidae) we find marked shortening of the jaws with reduction and great modification of the teeth. The dental formula is:

$$I \frac{3}{3}, C \frac{1}{1}, P \frac{3}{2}, M \frac{1}{1}, \text{total } 30.$$

The upper anterior premolar is often absent but otherwise the dentition is uniform throughout the family practically all of

which feed solely upon warm-blooded animals. In the Cats, therefore, the purely carnivorous dentition is seen in its full perfection.

In the domestic Cat, *Felis domesticus* (Fig. 62) the incisors are small and set transversely; the canines are long; the first upper premolar very small, often absent; the second larger, the third sectorial. The two lower premolars are comparatively simple and the second is the larger; the single upper molar ves-



Fig. 62.—Dentition of Cat (*Felis domesticus*, 9.7421-13). The Cats exhibit the extreme type of carnivorous dentition.

tigial and the lower sectorial. The last upper (sectorial) premolar shows a molariform appearance with a trigon and a metacone-metastyle shear. The lower molar, also sectorial, has lost all vestige of cusps save the protoconid and the paraconid which form a typical carnassial shear.

In this family as in the Carnivora as a rule the condyle is low and the palate terminates near the level of the last molar. It becomes apparent then that the low position of the condyle is the most satisfactory for the flesh-eater, and it is only in

those the diet of which is markedly omnivorous that the condyle rises. In the purely flesh-eating Mammals the glenoid fossa is a deep transverse groove permitting of no antero-posterior or lateral movement but this feature may also be distinct in others of the Carnivora which indulge in a more varied diet.

The Mustelidæ, called for the sake of simplicity the Weasels in the earlier part of the chapter, include many and varied genera which are very difficult to arrange. There are

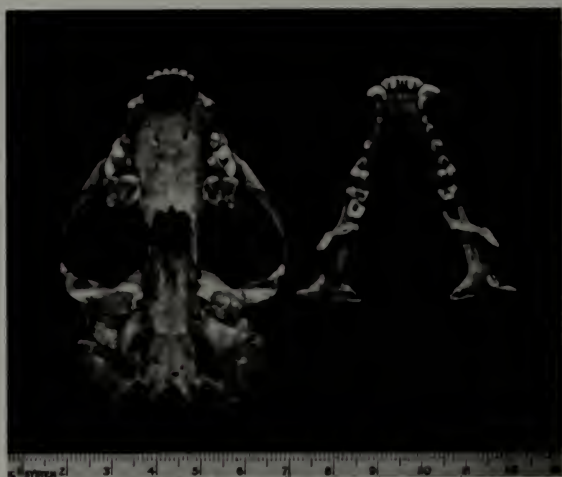


Fig. 63.—Dentition of Skunk (*Mephitis mephitis*, 9.7427-3). Note the peculiar form of the single upper molar. The second right lower molar is missing in this specimen.

otter-like, badger-like and weasel-like forms. In this account we can take only one and we choose therefore the common Skunk, *Mephitis mephitis* (Fig. 63) a member of the second group. Although because of the small size and fragility of the skulls of this family the records of its history are by no means complete we know from Oligocene ancestors that considerable changes have occurred in the skull during the evolution of the Mustelidae and that the skull is now much shorter than it was. In general the skulls of the Mustelinae are most like those of the

Bears and Raccoons but are readily distinguished from those of all other Carnivores by the peculiar shape of the single upper molar. The inner part of this tooth has a greater antero-posterior measurement than the outer part, although this character is not always very pronounced. In the Skunk, for example, it is slight.

The Skunk feeds on mice, frogs and eggs, worms, roots and berries, but in addition it destroys more insects than all our other Mammals put together. It is both arboreal and fossorial in habit. The dental formula is:

$$I \frac{3}{3}, C \frac{1}{1}, P \frac{3}{3}, M \frac{1}{2}, \text{total } 34.$$

The small transversely set incisors and the long canines both adapted for carnivorous food call for no comment. The premolars increase in size backward and are all simple except the last upper tooth which is sectorial though by no means pronouncedly so. The sharp cusps of the cheek teeth bespeak the pre-eminence of this animal as an insect-eater. The upper molar has a well developed external cingulum upon which the usual three styles can be distinguished; the internal cingulum rising into a hypocone behind is also very large. The lower molars resemble quite closely those of the Rasse already described but their cusps are not quite so needle-like. The first molar is not at all strongly sectorial; it possesses trigonid and talonid both with a full complement of cusps. The second as in *Viverra* is greatly reduced and exhibits practically only the talonid.

The next family to receive attention, the Raccoons or Procyonidae, is almost exclusively American, there being only one representative in the Old World, the Panda of the Himalayas. As already stated the family arose from the ancestors of the Dogs in the lower Miocene. One of the principal dental features of the early differentiation of the Raccoons was the change taking place in the sectorial fourth upper premolar. A

diminution in the sectorial character of this tooth began to occur together with the appearance of a postero-internal cusp. Other features were the corresponding diminution of the shearing edge of the first lower molar and the transformation of the first upper molar into subquadrate shape. Similar stages to these are even now to be observed in the comparison of the *Cacomistle* (*Bassaris*), the *Coati* (*Nasua*) and the *Raccoon* (*Procyon*) (see Fig. 100): the first shows a sectorial premolar



Fig. 64.—Dentition of *Coati-mundi* (*Nasua narica*, 9.7425-4). Note the diminution of sectorial features in the last upper premolar and first lower molar.

with a fair shear and no postero-internal cusp, and a first upper molar narrow antero-posteriorly; the second, diminution of the premolar shear with a small postero-internal cusp and a subquadrate first upper molar; the third, a greatly transformed premolar and a subquadrate molar.

As an example of the family we shall take the *Coati-mundi*, *Nasua narica* (Fig. 64) from tropical America. This is a gregarious beast, hunting in small troops and feeding upon fruits, young birds, eggs, lizards and insects. Its dental formula is:

$$I \frac{3}{3}, C \frac{1}{1}, P \frac{4}{4}, M \frac{2}{2}, \text{total } 40.$$

The incisors call for no comment but the canines are narrow, blade-like and characteristically turned outward. The four premolars increase in size and complexity from before backward, the last in each series being quite molariform. On the fourth upper premolar which has lost its sectorial character almost completely the small postero-internal cusp previously mentioned is apparent. The first upper molar is subquadrate with a hypocone of fair size; the second is smaller and tritubercular. The first mandibular molar presents a trigonid of which the metaconid is more prominent than the other two cusps and a large talonid the breadth of which is greater than that of the trigonid. The second is similar but has lost its paraconid and has a better marked hypoconulid upon its talonid.

The last family of the Fissipedia remaining for consideration is that of the Bears (Ursidae), which in spite of their present considerable differences in structure can be traced back to canine forms of the upper Miocene. The specimen figured is the somewhat deformed skull of a young female American Black Bear, *Ursus americanus* (Fig. 65). The example was chosen in spite of its defects, because the full quota of upper premolars is still present on the right side and the cusps of the cheek teeth are but little worn. The food of the Black Bear consists, according to Dr. Merriam, "not only of mice and other small mammals, turtles, frogs and fish, but also ants and their eggs, bees and their honey, cherries, blackberries, raspberries, blueberries and various other fruits, vegetables, and roots." The dental formula is:

$$I \frac{3}{3}, C \frac{1}{1}, P \frac{4}{4}, M \frac{2}{3}, \text{total } 42.$$

In the Bears the three anterior premolars are rudimentary

and are frequently missing; the second is lost in early adult life.

In the example figured one of the lower incisors is missing. The incisors and canines do not differ in any important particular from those of other Carnivores. Of the premolars the upper fourth calls for notice since it has lost its sectorial character and is a much simplified tooth. In the present specimen the premolars still in place on the right side are $\begin{smallmatrix} 1 & 2 & 3 & 4 \\ 1 & & & 4 \end{smallmatrix}$ and



Fig. 65.—Dentition of American Black Bear (*Ursus americanus*, 9.7426-6). Observe that almost all trace is lost of sectorial features in the teeth. Compare the molar crowns with those of the Baboon (Fig. 43).

on the left $\begin{smallmatrix} 1 & 3 & 4 \\ 1 & 2 & 4 \end{smallmatrix}$. The upper molars are elongated antero-posteriorly, especially the second, with low, rounded cusps on their crowns obviously very specialized, and the lower molars are also greatly transformed for, although the first and second show clearly their derivation from the typical form possessing trigonid and talonid each with the full complement of cusps, the third presents a crenated surface with no definite cusps.

The sectorial character of the first lower molar is almost completely absent.

In the Bears as in the other families different species exhibit various stages of specialization and adaptation but we have already sufficiently emphasized this point in discussing previous groups.

The Pinnipedia

The history of the aquatic Carnivora is almost a blank page in paleontology and we know but little of their affinities. It has been suggested that they are related to the early Creodonts. Of late the Creodont theory has been displaced by one which would derive them from some form related to the "Bear dogs" of the Miocene but this suggested origin again is not very clearly demonstrated. Certain resemblances which may imply a relationship to the Walrus have been pointed out by Dr. Matthew in the Eocene Insectivore *Pantolestes*. We can only say at present that there is no doubt that the forerunners of this order were terrestrial Mammals with a typical and complete dental formula and furthermore that it does not take very long, geologically speaking, for a tritubercular molar to retrogress into a simple conical tooth.

Of the Pinnipedia there are three existing families, the Sea-lions, Walruses and Seals, of which the last mentioned are in general the most specialized. Nevertheless the Walrus has a curiously aberrant dentition and in this feature must take the place furthest from typical Carnivora.

The Sea-lions, least aberrant of the group, are represented in Fig. 66, which is an illustration of the jaws of the common Gillespie's Sea-lion, *Zalophus californianus*. This animal in its general anatomical characters is the least removed of all the Pinnipedia from the terrestrial Carnivora. In most members of the suborder the milk teeth are shed about the time of birth, but in *Zalophus* they remain in situ for a few weeks. The food of this animal consists of fish, molluscs and sea-fowl. The dental formula is:

$$I \frac{3}{2}, C \frac{1}{1}, P \frac{4}{4}, M \frac{1}{1}, \text{total } 34.$$

The third upper incisor is caniniform, each of the others shows a well-marked notch on the crown somewhat similar to that observed in terrestrial Carnivora. The lower incisors are slightly procumbent. The canines are stout and slightly compressed, the upper ones vertical, the lowers directed somewhat outward. The premolars and molar of the maxilla are secondarily simple teeth each with a well-marked cingulum surrounding the base of the crown. Their single cusp probably

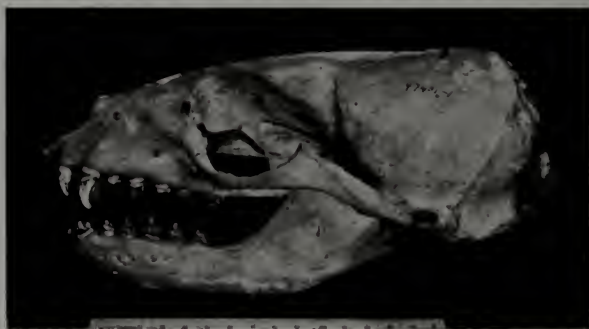


Fig. 66.—Lateral view of skull of Gillespie's Seal-lion (*Zalophus californianus*, 9.7451-1). Note the secondary reversion of the cheek teeth to conical form.

represents the paracone. The mandibular cheek teeth are also simple but the basal cingulum rises into a small cusp in front and behind the apex of the tooth which may be the homologue of the protoconid.

The Seals differ quite considerably according to species in the number of their incisors and their cheek teeth show varying degrees of reduction to a simple or a secondarily triconodont form. The fact that great variation occurs even among individuals indicates that this family is even now evolving at a rapid rate.

The Walrus, *Odobenus rosmarus*, is a gigantic animal living

on bivalved molluses, shrimps, sandworms and starfishes, Its functional dental formula is:

$$I \frac{1}{0}, C \frac{1}{1}, P \frac{3}{3}, M \frac{0}{0}, \text{total } 18.$$

In the young, however, the dental formula is:

$$I \frac{2}{2}, C \frac{1}{1}, P + M \frac{5}{4}, \text{total } 30.$$

All the teeth are secondarily simple and retrogressed save the enormous upper canines which are almost as long in the female as in the male and are used by the animal in digging up molluses from the mud and in clambering over the ice.

CHAPTER XI

THE RODENTS

A STUDY IN THE EVOLUTION OF HERBIVOROUS TYPES

Rodent suborders—History of the *Simplicidentata*—Primitive modern squirrel-like forms—The adaptation of the Rat to an omnivorous diet—Increasing specialization in the *Porcupines*—Extreme herbivorous adaptation in the *Patagonian Cavy*—Dentition of the *Rabbit*—History of the *Duplicidentata*—Convergent evolution in Rodents, *Marsupials* and *Primates*.

The Rodents, the skulls of which are easily distinguished by chisel-like incisors and the hiatus between these and the cheek teeth, are of world-wide distribution, some even having reached Australia. So numerous and varied are they that it is impossible to describe them adequately within the restricted compass of this volume. The best we can do is to indicate the general trend of evolution within the order.

As a group the Rodents are separated into two suborders. The Rabbits, Hares and *Pikas* which have two pairs of upper incisors are termed *Duplicidentata* whereas the *Simplicidentata* possess only a single pair of upper incisors. The latter suborder includes the following sections: *Sciuromorpha*, squirrel-like; *Myomorpha*, mouse-like; and *Hystriecomorpha*, porcupine-like Mammals. Of these the *Sciuromorpha* are the most primitive and the *Hystriecomorpha* the most highly specialized.

Even in the *Oligocene* the *Duplicidentata* were almost as greatly differentiated from contemporary *Sciuromorpha* as at the present date. Hence the two suborders must have had

independent histories from at least the Basal Eocene, a great length of time which has permitted the appearance of many convergent characters.

In the Basal Eocene we find the Rodents had already attained obviously ordinal characters as in the case of the Bats, the Edentates, the Cetacea and all the Ungulate orders except the Artiodactyla. Therefore we must infer that the point of divergence of the Rodents from the general mammalian ancestors must lie well back in Cretaceous times. It is this order which, above all among Placentals, shows most the influence of the incisor modification in determining the characters of the dentition. We believe the ancestral Rodents were semi-arboreal Mammals with rather large procumbent incisors as in some modern Insectivores, canines and anterior premolars reduced and bunodont molars adapted for an omnivorous diet. The Eocene genus *Paramys* displays characters of this nature.

Starting as we have usually done with a less specialized form we shall describe the dentition of *Arctomys* first.

Arctomys monax, the Woodchuck or Ground Hog (Fig. 67), is a Marmot of burrowing habit and lives upon grass and clover. Although fossorial it can and does climb trees both for pleasure and for protection. The Rodent features of the skull are recognized at once. Its molar teeth do not greatly differ from the typical mammalian form, the hinder ends of the upper tooth rows converge but slightly and the palate ends a short distance back of the last molar, three features previously noted as indicating a comparatively slight degree of specialization. The tooth formula is:

$$I \frac{1}{1}, C \frac{0}{0}, P \frac{2}{1}, M \frac{3}{3}, \text{total } 22.$$

The specimen photographed is not a completely adult skull: the first lower and the anterior upper cheek teeth belong to the milk dentition and are replaced in later life by stouter and more molariform premolars. The incisors are enamel-

coated only in front and laterally, uncompressed, broad and powerful, beveled upon their posterior aspect and strongly curved so that the persistently growing roots are not subject to injury. This method of protecting tooth roots from pressure insults is also seen to some extent in the molars but the curvature is much more strongly marked in the cheek teeth of the Wombat (page 90). The premolars and their milk predecessors have already been mentioned. Although the first milk tooth in the upper jaw is very small it is replaced by a much



Fig. 67.—Dentition of Woodchuck (*Arctomys monax*, 9.3213-1). This is the skull of a young animal. The first and second upper and the first lower cheek teeth belong to the deciduous dentition. Observe the characteristic Rodent incisors and glenoid fossae and also the relatively slight divergence from the primitive mammalian molar pattern.

larger and molariform premolar. At first sight the molar crowns do not appear to resemble at all closely the typical mammalian pattern. If however the first and second upper molars be examined with care it will be seen that they exhibit a well-marked protocone from which ridges pass laterally to the paracone and the metacone and that about midway along the hinder ridge there is a clearly marked metaconule. Already in the Marmot the crown is complicated by the occur-

rence of anterior and posterior cingula or accessory ridges running laterally, the anterior terminating in a small buccal parastyle, the posterior fading away as it nears the metacone. There is no hypocone. In the case of the third molar the metacone region is enlarged so that this tooth is the largest of all, a character which may be primitive since the molars increase progressively in size from before backward but on the other hand, may be secondary indicating the commencement of the well recognized herbivorous specialization previously noted on several occasions. The crowns of the lower molars are rhomboidal with a basin-shaped talonid presenting hypoconid and entoconid. The anterior edge of the tooth shows a small lateral protoconid and a larger lingual cusp, the homology of which is obscure for its position indicates that it may represent the paraconid, the metaconid or these two cusps fused together. Here, again, the last tooth is the largest.

The rhomboidal character of the lower molars is explained by the obliquity of the masticatory movements. Antero-posterior motion of the jaws can only take place when the incisors alone are used in gnawing. In such movements the incisors by mutual grinding come to bevel each other upon the posterior face; the molars are not in occlusion. Great elongation of the glenoid fossa in the antero-posterior direction permits free gnawing movement and the lips, sinking deeply their internal hair covered surfaces into the hiatus between incisors and cheek teeth, prevent any chips entering the mouth proper.

In spite of the fact that the Woodchuck is largely a grass feeder its molar teeth are brachydont and do not possess permanent tooth pulps. These features it shares with its Old-World relations, the food of which consists of roots, leaves and the seeds of various plants.

In the photograph of the dentition of the common Brown Rat, *Mus norvegicus* (Fig. 68) representing the *Myomorpha*, it is seen that the tooth formula is:

$$I \frac{1}{1}, C \frac{0}{0}, P \frac{0}{0}, M \frac{3}{3}, \text{ total } 16.$$

This dentition is more specialized than that of the Sciuro-morpha since the milk teeth never appear and the typical mammalian pattern of the molars is more obscured. The Rat is an omnivorous feeder and its brachyodont and bunodont molars are tuberculated in a fashion somewhat similar to those

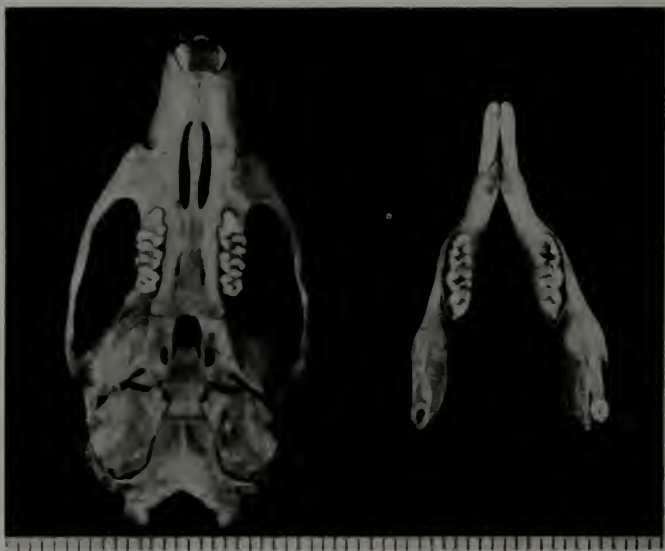


Fig. 68.—Dentition of Brown Rat (*Mus norvegicus*, 9.3212-2). Note the tuberculated swine-like features of the cheek teeth.

of the Pig. The parallel rows of cheek teeth, the retention of a small third molar and the formation of the palate are relatively unspecialized features. The first molar in this animal on the other hand is considerably enlarged.

We pass next to the Hystricomorpha and take for our example *Coendou prehensilis*, the Tree Porcupine of Brazil (Fig. 69). This arboreal animal feeds upon the leaves, young shoots and bark of the trees in which it lives. The tooth formula is:

$$I \frac{1}{1}, C \frac{0}{0}, P \frac{1}{1}, M \frac{3}{3}, \text{total } 20.$$

Both cheek teeth and palate show greater specialization than in the foregoing representatives of the order. The palate is narrow and terminates at the level of the interval between the second and third molars. The incisors are somewhat compressed and the premolar in each jaw is completely molariform. The complexity of the molars is not so baffling as at first ap-



Fig. 69.—Dentition of Brazilian Tree Porcupine (*Coendou prehensilis*, 9.3213-2). In spite of the growing complexity of the crown pattern in the cheek teeth there are not yet persistently growing or fully curved roots as in the following example (Fig. 70).

pears to be the case. As in the Kangaroos the two inner cusps (protocone and hypocone) in the upper molars and the two outer cusps (protoconid and hypoconid) in the lower teeth are connected by antero-posterior ridges. In both jaws these two cusps can thus be distinguished. The upper molars present anterior and posterior cingula both proceeding laterally, the former from the protocone, the latter from the hypocone; separated from these and from each other by deep grooves are the ridges running to the paracone and the metacone respec-

tively. In the lower molars the same four cusps seen in *Arctomys* can again be identified. All the cheek teeth are subequal in size and though they are brachyodont and do not possess permanent pulps they begin to show that curvature of root and obliquity of occlusal surface so pronounced in the type next to be considered and indicating Nature's method of protecting the growing root from injury.

As representing the most advanced type of Rodent dentition among the *Simplicidentata*, we have chosen *Dolichotis*



Fig. 70.—Dentition of Patagonian Cavy (*Dolichotis patachonica*, 9.3213-6). This extreme type of placental Rodent should be compared with the similarly extreme Marsupial *Phascolomys* (Wombat, Fig. 28).

patachonica, the Patagonian Cavy or Mara (Fig. 70). In habits and general appearance this animal resembles the Hare but its legs are longer and its ears are shorter and broader. It is essentially a grass feeder but will also eat roots and stems of such plants as grow near its burrow. Very marked specialization is seen in the greatly restricted palate, the abutting against one another of the upper cheek teeth rows in front, and in the double columnar cheek teeth. These are hypsodont, possess per-

manent pulps and are curved, the concavity of the uppers as usual being directed outward and that of the lowers inward. Otherwise the description already given of the Wombat's cheek teeth will suffice for these (page 91) except that the single premolar is completely molariform and does not resemble merely half a molar as in the Wombat while the upper molars increase in size from before backward.

We now take up the study of the teeth of the *Duplicidentata* but shall examine only a single representative, namely the



Fig. 71.--Dentition of Northern Cottontail (*Lepus floridanus transitionalis*, 9.322-1). In this very specialized form the distance between the rows of mandibular teeth is less than that between the maxillary tooth rows. Hence in the Rabbit as in Ruminants, mastication takes place on one side of the mouth only at one time.

Northern Cotton-tail, *Lepus floridanus transitionalis* (Fig. 71) a grazing animal which is by no means averse to roots, stems and bark also. The dental formula is:

$$I \frac{2}{1}, C \frac{0}{0}, P \frac{3}{2}, M \frac{3}{3}, \text{total } 28.$$

The large anterior upper incisors show a well-marked groove on their labial surface. Behind each of these teeth is the diminutive posterior incisor. The cheek teeth are all molariform in

both upper and lower jaws and the third molar in each case is the smallest. Both premolars and molars are hypsodont and resemble the corresponding teeth of *Dolichotis* but the columns are much more closely pressed together so that the antero-posterior diameter of each tooth is much less than the transverse. The teeth all have permanent pulps, exhibit enamel on the anterior face only and show the curve characteristic of an advanced Rodent dentition. In one respect the Rabbit has progressed far beyond any of the *Simplicidentata* for in all Rodent types so far considered the occlusion of upper and lower cheek teeth of one side necessarily involved occlusion upon the other also; it is not so in the Rabbit in which the distance between the two rows of mandibular cheek teeth is less than that between the rows of teeth in the upper jaw. This condition is also observed in the Ruminants. In the Rabbit, mastication can proceed upon one side only of the mouth at a time; upper and lower cheek teeth are not in occlusion upon both sides at once.

Upon tracing back the cheek teeth of the Hares in paleontological history it has been found that the enamel was not always confined to the anterior aspect of the tooth, that the deep notches on the internal and external faces are also secondary, that the single root with its permanent pulp was preceded in geological times by a three-rooted type and that the whole tooth was formerly less hypsodont. Already in the Oligocene the extent of the enamel was becoming reduced and the two lateral roots growing more rudimentary whereas the internal attained a proportionately greater size and importance. The tritubercular form of the upper molar has become obscured in the course of time and the complexity of the crown increased by the addition of a large cingulum which composes the inner part of the tooth. The cheek teeth of the milk dentition still exhibit vestiges of a tritubercular crown and this makes it the more probable that the permanent teeth were of a similar appearance. In spite of the present peculiar pattern therefore we may feel confident that before the ancient separation of Rodents into

the two great suborders the ancestors of the Duplicidentata possessed cheek teeth not differing greatly from those exhibited today in *Arctomys* and other sciurid forms.

In thus reviewing rapidly the various forms of teeth met with in modern Rodents we note that there are different degrees of specialization, the most pronounced differing considerably from the typical mammalian pattern but the less pronounced approximating fairly well to the general type. It is also known that the general type was still more approximated in the Eocene *Paramys*. Some authors believe on both paleontological and embryological grounds, however, that the Rodent dentition in its ancestry does not approximate but rather differs more pronouncedly than it does today from the tritubercular tuberculo-sectorial type. There undoubtedly are difficulties in the way of accepting the typical mammalian molar form as ancestral to that of the Rodent but these are gradually disappearing as we obtain more knowledge of early members of the order. Since the history of the Rodents must extend back even into Cretaceous times there has been ample opportunity for modification of tooth forms.

Another significant fact upon which emphasis has been laid from time to time in foregoing chapters, a fact which will not therefore be labored at the present, is the striking similarity of dentition called forth by similarity of environment and habit in advanced Rodents, in certain Marsupials notably the Wombat, and in the Primate Aye-aye (see pp. 90, 115). It is worth while remembering that the two land areas, not penetrated to any great extent by Rodents of which order South America is at the present time the headquarters, are Australia and Madagascar and that it is in these two regions that the Wombat and the Aye-aye respectively have developed through convergent evolution.

In noting the several adaptations of the Rodents to a completely herbivorous diet we have touched upon certain features which we shall find reproduced in the Ungulate orders. These

are the increasing complexity of molar pattern, the molariform character of the premolars, the hypsodont evolution in the cheek teeth with their persistently growing roots and the relative narrowing of the mandible associated with mastication upon one side only at once. It was the study of these features which so strongly impressed Huxley and led him to declare that anyone who knew the modifications which appear in the Insectivore and Rodent dentitions knew also the range of modification of teeth in all other mammalian orders.

CHAPTER XII

THE ARTIODACTYL UNGULATES

Ungulates in general—Differences between Artiodactyls and Perissodactyls—The Pigs and Hippopotamus—Camels and Llamas—Divisions of the Pecora—Deer and Giraffes—The hollow-horned Pecora—Paleontological history of the Artiodactyls.

THE UNGULATES IN GENERAL

Hoofed animals or Ungulates are a numerous and very varied throng of Mammals from among which can be separated the even-toed Artiodactyls and the odd-toed Perissodactyls but there still remain among modern types the Elephants and the Hyrax, the former representing the remnant of a once numerous group, the latter a quaint and zoologically isolated form.

Broadly speaking the distinction of Artiodactyls and Perissodactyls as even-toed and odd-toed Ungulates respectively is doubtless good enough but for scientific purposes a more precise definition would be: that whereas, the axis of the foot in the Perissodactyls passes through the third digit, in the Artiodactyls it runs between the third and fourth which together form the irreducible minimum.

But it is not merely in the feet alone that these two groups differ from each other. The skeleton and soft parts of the Perissodactyl show significant differences from the corresponding structures in the Artiodactyl and what is more striking the several parts of the body are wonderfully alike within each of these orders although belonging to animals very various in external form. There is not space nor would it be profitable in the present connection to discuss these differences in detail.

Suffice it to say that so far as teeth are concerned the premolars and molars in the Artiodactyls are never alike as a series and only rarely does the last premolar ever become molariform. In the Perissodactyls, on the contrary, all the premolars except the first are molariform in size and in appearance. Further, throughout the entire history of the two orders so far as it is known at present these differences have existed. In the most ancient examples of the Artiodactyls the premolars are simple, the fourth being at most bicuspid; the upper molars are tritubercular and the lowers very like typical tuberculo-sectorial teeth, whereas the oldest Perissodactyls already show a molariform appearance in the posterior premolars, quadritubercular upper molars and lowers with commencing lophs.

ARTIODACTYLA, THE EVEN-TOED UNGULATES

Included within the order Artiodactyla are such diverse animals as Pigs and Hippopotami; Camels and Llamas; Deer and Giraffes; Antelopes, Sheep, Oxen and Goats; an aggregation strange and varied enough yet in structure showing remarkable unity and clearly defined distinctions from members of all other orders.

Among these creatures we find two types of molar, the bunodont and the selenodont, together with varied degrees of hypsodonty. It is often said that of the two types the bunodont is the more primitive and that from it the selenodont differentiated, but however this may be, the latter type dates back to the dawn of Artiodactyl history. In other orders we have already seen the formation of the selenodont type through the utilization of styles but it will be recalled that this development was true of the upper molars only. The production of the crescents of the lower molars was rather directly from the drawing out of the edges of primitive cusps possessing the shape of a three sided pyramid. It is probable that the Artiodactyl crescents were formed in a similar manner for the most ancient members of this order and of the Perissodactyla also

exhibit molars, the protocone and protoconid of which are not round but already somewhat crescentic in shape.

SUIDAE

First among the Artiodactyla we take the Pigs and the nearly related Hippopotami. The former family includes the Swine of the Old World and the American Peccaries together with a vast number of other forms now extinct. The original placental formula:

$$I \frac{3}{3}, C \frac{1}{1}, P \frac{4}{4}, M \frac{3}{3}, \text{total } 44.$$

is found in some species of this family although frequently the more anterior premolars tend to be lost.

We must pass over the Peccaries which are close relations of the true Swine, more primitive in some respects and more advanced in others but with simpler molars and non-everted canines.

The example chosen to represent the Suidae namely the Red River Hog, *Potamochoerus porcus* of West Africa (Fig. 72) shows molar teeth in some respects simpler than those of the common domestic Pig, for they are less tuberculated and the last lower molar is not so elongated. This animal lives in moist forests and on river banks and like other members of the family feeds upon roots and carrion. The dental formula is:

$$I \frac{3}{3}, C \frac{1}{1}, P \frac{3}{3}, M \frac{3}{3}, \text{total } 40.$$

The median upper incisors separated at their bases and approximating at their tips, and the procumbent lower incisors recall the arrangement already noted in Marsupials and to a less extent in Insectivores. The canines have persistently growing roots, are tusk-like and very specialized. Both upper and lower tusks project laterally and are triangular in section.

The enamel on the distal aspect of the upper canine is arranged in three ridges; the distal aspect of the lower canine is devoid of enamel. The rows of cheek teeth are almost parallel and the palate terminates behind the last molar. The premolars in both jaws increase in size and complexity from the simple first to the molariform last. A molariform crown even for the last premolar is by no means common among the Artiodactyla. The most anterior lower premolar (P2 of the primi-



Fig. 72.—Dentition of Red River Hog (*Potamochoerus porcus*, 9.731-1). This animal possesses a dentition more primitive in certain respects than that of the domestic Pig. The rounded cusps and accessory cuspules on the molars and the elongation of the last molar indicate the root diet. Compare the dentition of the Baboon (Fig. 43).

tive placental dentition) is lost relatively early in life. The molars are brachyodont, bunodont and quadricuspid in form, the paraconid of the lower teeth being absent. But the well-rounded appearance of the cusps like the multitude of additional cuspules is secondary in character and related to the type of food eaten. So also is the marked elongation of the last molar in each jaw, the extension of the talon and the tal-

onid, as in the Kangaroos and more especially in the Baboon, indicating a herbivorous diet.

We can only glance briefly at the Hippopotamus which again possesses molars the bunodont cusps of which are obscured as in the Pig by many secondary cuspules tending to convert them into lophs. The crown of each molar presents therefore a double trifoliate appearance. Such crowns are excellently adapted for masticating the roots of succulent water weeds torn out by the tusks of the animal. The dental formula is:

$$I \frac{2}{2}, C \frac{1}{1}, P \frac{4}{4}, M \frac{3}{3}, \text{total } 40.$$

The incisors and the canines, the latter supported on special bosses of bone, are all tusk-like in appearance and possess persistently growing roots to compensate for the marked attrition to which they are subjected in uprooting the vegetation upon which the animal feeds. As in the Pig the median upper incisors approximate at their tips and the lower teeth are procumbent. Again, as in the Pig, the canines are trihedral. The premolars, of which the first is lost early are all simpler in form than the molars. All the cheek teeth are subject to great wear from the large amount of sand and grit among the food. The first molar which erupts considerably before the others shows this wear strikingly. The structure of the molar crowns has already been noted together with the numerous secondary cingules and cuspules. The last lower molar possesses a backwardly extended talonid. The rows of cheek teeth are approximately parallel and the palate terminates just behind the third molar.

The elevated position of the ear-holes and orbits and the dorsal situation of the nostrils in the Hippopotamus indicate an aquatic habit, the animal floating entirely submerged save for its ears, eyes and nose.

TYLOPODA

Passing next to the Camels and Llamas we find that the history of these animals is fairly well known. Their ancestors diverge from those of the Pecora (Deer, Antelopes, etc.) about the middle Eocene and hence the many points of similarity such as the selenodont and hypsodont teeth found in both these groups must obviously be examples of parallel evolution rather than heritages from a common forerunner.

The history of the Camels and Llamas moreover shows that the development of this group occurred almost wholly in North America, the Camels for some reason at the present unknown ultimately migrating to Asia and the Llamas to South America. The Pecora, on the other hand, are a typically Old-World group.

Differences between the Camels and Llamas are largely superficial, depending upon character of hair, length of ears, general build and the presence in the one group and absence in the other of humps, masses of fat which are naturally unrepresented in the skeleton. Apart from size, certain minor distinctions and the absence of the two anterior upper premolars, the skeleton and teeth of the Llama are closely similar to those of the Camel.

In both animals the skull appears triangular through the abrupt narrowing of the facial region. The orbits are surrounded by bony rings and the neck is strikingly long as in the Giraffe. The dental formula in the Camel (Fig. 73) is:

$$I \frac{(3)1}{3}, C \frac{1}{1}, P \frac{3}{2}, M \frac{3}{3}, \text{total } 34.$$

The first and second upper incisors are lost very early but the third, the canine and the first premolar are long and sharp teeth capable of giving a very serious bite. The lower incisors are procumbent, large, spatula-shaped and overlapping; the lower canine vertical and standing apart from the incisors. The second premolar is missing and the third and fourth each somewhat resemble the half of a molar; the third premolar like the

first and second incisors is lost early. The molars are selenodont but not markedly hypsodont. Each is quadricuspid. In the upper molars the three primary cusps and the hypocone are all present; in the lowers the paraconid is unrepresented but the other four cusps of the primitive tuberculo-sectorial tooth



Fig. 73.—Dentition of Camel (*Camelus* sp., 9.7355-1). Here are seen reduction of the upper incisor series, commencing hypsodonty of the cheek teeth, narrowing of the mandible and elongation of the last lower molar which occur in more pronounced form in Deer and Oxen.

exist. The obliquity of setting of the upper molars in the jaw so that the antero-lateral corner of the one projects beyond the postero-lateral corner of the tooth in front is a feature shared in common with the Pecora and characteristic of the ruminant

habit. The last lower molar has a talonid extended somewhat by the addition of an extra cusp but this cusp is smaller than is the case usually among the Pecora. In addition to the overlapping upper molars, the extension of the last lower molar and the general hypsodont character of the teeth there is another feature in which the dentition of the Camel resembles that of the Pecora. This is the relative narrowness of the mandible compared with the breadth of the palate. In consequence the upper and lower cheek teeth of one side only can enter into contact at one time: on the opposite side the upper cheek teeth project so far beyond those of the lower jaw that there can be no occlusion. Thus the Camel like the Deer and the Cow masticates first upon one side of the mouth and then upon the other.

PECORA

The Pecora or true Ruminants, all of them browsing or grazing animals of Old-World origin, are the most specialized and varied of the Artiodactyla. All are alike in the absence of upper incisors and, with the exception of some Deer, of the upper canines also. The lower canines are always incisiform; the number of premolars three in each jaw and the molars invariably selenodont. The usual four cusps are present on the crown of each upper and each lower molar as in the Camel. The paraconid alone is lost. The last lower molar presents an additional cusp on the talonid, relatively larger than that present in the Camel, thus exhibiting, as previously observed, a typical herbivorous specialization. But this additional cusp is not invariable in the Pecora: it is absent in Salt's Antelope one species of the genus *Neotragus*, and is rudimentary in other species of this genus and in the Gnus.

The Pecora are subdivided into the solid-horned type or Cervicornia comprising the Deer and Giraffes, and the hollow-horned or Cavicornia including Antelopes, Sheep, Goats, Oxen and Buffaloes. The latter group is of comparatively recent

origin, the earliest fossil remains dating back no further than the Miocene.

As an example of the Cervicornia we take the black-tailed Virginia deer, *Odocoileus hemionus* (Fig. 74), a genus which has changed very little since Pliocene times. The skull is that of a young doe but shows by the relative wearing of the teeth how much later than the first the third molar erupted. The dental formula is:

$$I \frac{0}{3}, C \frac{0}{1}, P \frac{3}{3}, M \frac{3}{3}, \text{total } 32.$$

Of the lower incisors, which with the incisiform canines* are

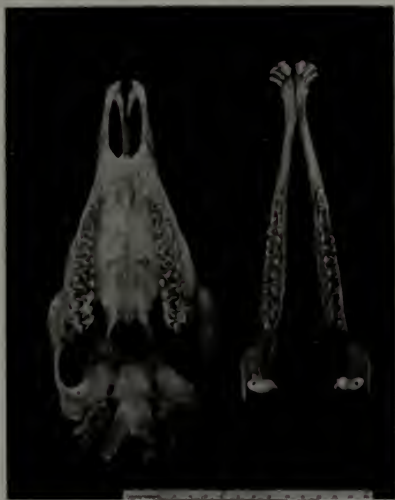


Fig. 74.—Dentition of Black-tailed Virginia Deer (*Odocoileus hemionus*, 9.7351-7). In this example of Ruminant dentition can be observed in more pronounced degree the features already noted in the Camel. The specimen is a young one and still retains in front of the permanent molars the three milk molars which precede the premolars. The lower permanent canines are lost.

procumbent, the median pair is much the largest. No trace of the upper canines exists. There is a considerable interval between the incisors and the cheek teeth, the maxillary series of

*The canines are lost in the specimen figured.

which possesses broader crowns than the mandibular. The three premolars increase in complexity from before backward but not even the last becomes truly molariform:* each of the upper premolars resembles half a molar. The cheek teeth are plainly selenodont but the valleys between the cusps are only partially filled with cement. The teeth cannot be called truly hypsodont and indeed the first molar at least in all Cervidae is obviously brachyodont. The upper molars show the typical ruminant obliquity of setting. A small globular style occurs in the transverse furrow on the inner side of the first upper



Fig. 75.—Lateral view of skull of Musk Deer (*Moschus moschiferus*, 9.7351-15). Note the elongated upper canines and the short crowned cheek teeth.

molar and the outer side of each lower molar. An extra cusp is present upon the talonid of the last lower molar, producing elongation of this crown as already noted above. Mastication takes place on one side only at a time, a feature common to all the Ruminants.

Before passing to the Cavicornia it is worth while glancing for a moment at the skull of the Musk Deer (Fig. 75), an animal more primitive in many respects than the true Deer and one

*In the specimen figured the premolars have not yet erupted; their place is occupied by the deciduous molars.

which has progressed along lines of its own. Note the brachydont-molars and the enormous size of the upper canines which are especially tusk-like in the male though present in both sexes. The elongation in the male may be associated with absence of horns. The chief diet of the animal consists of young twigs and buds in the birch forests of the Himalayas above the zone of pines.

Of hollow-horned Ruminants, though the number of species is very extensive, space will permit us only one example, namely, the domestic Cow, *Bos taurus* (Fig. 76). The skull illustrated is that of a young animal between two and three years of age. The dental formula of the Cow like that of all Pecora is:

$$I \frac{0}{3}, C \frac{0}{1}, P \frac{3}{3}, M \frac{3}{3}, \text{total } 32.$$

In the specimen figured the milk canines and the predecessors of the upper and lower third premolars together with that of the second left upper premolar are still in situ. In general the dentitions of the Cow and of the Sheep are very much alike but in the former the incisors are less firmly imbedded and the cheek teeth have a well marked accessory style not present in the latter. Most of the remarks already made regarding the dentition of the Deer may be applied with equal justice to that of the Cow. Regarding the absence of upper incisors and canines it may be mentioned that embryological investigation shows that in the Cow as in the Deer the upper canines were the last teeth to be lost. The valleys between the cusps on the crowns of the bovine cheek teeth have a greater amount of cement than those of the Deer. The last lower molar presents a well marked extra cusp on the talonid. The style present in the deep furrow notching the palatal aspect of the upper molars shows very well the pronounced amount of wear in these hypsodont teeth. In the specimen figured the style on the first molar, which erupted long before the others, is already considerably worn. In the second molar

where there is much less attrition, the style is seen emerging beyond the bony palate and the tooth is not yet worn to the level of its apex. In the third molar which has only just erupted the style is still imbedded in the maxilla.

The origin and divergences of this extensive order are



Fig. 76.—Dentition of domestic Cow (*Bos taurus*, 9.7354.9). Note the small lower deciduous canine (lost on the right side), the third deciduous molars (removed on one side to show the erupting premolar beneath) and the second upper left deciduous molar.

interesting though largely obscure. We have already noted that the Camels and Llamas separated from the main stock at least as far back as the middle Eocene. Somewhat later, in the middle Oligocene, the Cervicornia and Cavicornia diverged from each other. From the former the Giraffe originated and became very widely distributed in the Miocene. In this epoch

also the first Cavicornia appeared but they formed no extensive group until the Pliocene when the number of species greatly increased with Asia as a center of radiation.

As regards origin we have previously seen that even in the earliest examples the Artiodactyla are quite clearly distinguished from the Perissodactyla, that resemblances between these two orders are the result of parallel or convergent evolution and that any heritages which they may possess in common are merely those derived from a protungulate stock. Some authors have suggested a genetic relationship between the primitive Artiodactyls and the Insectivores and Primates but such similarities as occur are merely superficial and probably do not point to phylogenetic connections. Far more likely is it that the Artiodactyla are originally related to unknown Basal Eocene Creodonta which, however wide the difference between modern Artiodactyls and this extinct and usually carnivorous suborder, foreshadowed many of the features found in the primitive Artiodactyla. In a previous chapter we have noted that the fissipede Carnivores of today probably arose from a family of Creodonts known as the Miacidæ. The Artiodactyl Ungulates have no connection with this family but with another Creodont group, the Mesonychidae which were animals developed for great speed, possessing broad blunt claws and probably already vegetarian in habit.

CHAPTER XIII

THE PERISSODACTYL UNGULATES

Great divergence within the order—History of the Tapirs—
The Rhinoceroses—Paleontological record of the Horse—
Features of the equine dentition—Ancestral relationships
of the order.

Perissodactyla the zoological term for the odd-toed Ungulates must not be taken to mean literally that representatives invariably possess an odd number of toes, the Tapirs for example having four toes on the forefeet. Rather, as previously pointed out, the term must be construed as indicating that the axis of each foot is formed by the third digit. Included within this order are the modern Tapirs, Rhinoceroses and Horses but in ancient times it comprised also many other families, some of them quite grotesque in appearance. Different as the three modern representatives are from each other today their lower Eocene fore-runners are clearly of common stock. Starting from unknown but common Cretaceous ancestors, the Perissodactyls developed into a great multitude of varied forms of which the existing representatives are a mere handful.

Of modern forms the Tapirs have changed least; they remain almost as they were in Miocene times. Indeed we must compare the modern with the Oligocene Tapirs if we desire to see any marked differences in skeletal structure. From reference to these early forms we note that the main dental change which has occurred in developmental progression with increase in size of the animal is approximation to the molar pattern of at first only the hindmost premolar but ultimately and at the present day of all except the first, together with reduction in size of the upper canine and consequent enlargement of the

third upper incisor. All the cheek teeth are low crowned for the Tapir is a forest animal browsing upon shoots, buds and leaves. Its dental formula is:

$$I \frac{3}{3}, C \frac{1}{1}, P \frac{4}{3}, M \frac{3}{3}, \text{total } 42.$$

The skull figured is that of a young specimen of the so-called Indian Tapir, *Tapir indicus* (Fig. 77) which, however, is found not in India proper but in the Malay Peninsula, Suma-



Fig. 77.—Dentition of Asiatic Tapir (*Tapir indicus*, 9.721-1). This is a young animal in which the permanent dentition is just beginning to replace the milk teeth. The only representatives of the permanent set erupted are the first and second incisors and the first molars. All the other teeth are deciduous. This figure should be examined in connection with the Premolar Analogy Theory (see pp. 61, 103). Note that the elongation of the crowns of all the milk molars and of the first permanent molars lies in the cusps rather than in the tooth bodies.

tra and Borneo. In consequence of its youth the third upper incisor is only just erupting, the upper canine and second and third molars of both jaws are still unerupted, and the lower

third milk incisors, canines and all the milk molars are still in place.

One of the most interesting and significant features of the Tapir dentition is the occurrence, according to the late Dr. Ameghino, of at least one functional premilk tooth in the premolar region. To this we shall refer later in the chapter upon the deciduous dentition. The low-crowned molars of both jaws show the formation of transverse crests or lophs through the union of anterior and posterior pairs of cusps, a conformation of occlusal surface evolving in browsing species of many mammalian orders. The elongated or hypsodont character of the loph associated with the brachyodont bodies of the cheek teeth is very noticeable; it recalls the similar arrangement in the Kangaroos. The four cusps presented by each of the upper teeth are those of the trigon with the addition of the hypocone and in the lower teeth the proto-, meta-, hypo-, and ento-conids, the paraconid as usual being lost. Well-marked anterior and posterior cingula are to be seen on all molars. There is also a poorly marked external ridge or ectoloph connecting paracone and metacone of the upper molars.

The Rhinoceroses form one of the largest and most complicated groups of Mammals provided one include all extinct species. No less than seven phyla flourished at various times and of these three exist today. In addition there were two other series allied to the Rhinoceroses in the Eocene and Oligocene periods, one a lightly built cursorial form, the other heavy and aquatic.

So far as teeth are concerned the modern type was reached in the Pliocene. All Rhinoceroses have low-crowned browsing cheek teeth except the White or Square-lipped Rhinoceros of Africa, a grazing variety with fairly hypsodont molars which has lost all its incisors and canines above and below. The dental formula is:

$$I \frac{1}{2} \left(\text{or } \frac{0}{0} \right), C \frac{0}{0}, P \frac{4}{4}, M \frac{3}{3}, \text{ total } 34 \text{ (28)}.$$

The broad upper incisor with its oblique chisel-shaped edge shears against the lower lateral tusk-like incisor. The premolars except the first are similar in appearance to the molars though somewhat smaller. The upper molars show obliquely placed lophs, not transverse as in the Tapirs, and the ectoloph connecting the paracone and metacone is well marked. Each lower molar exhibits a double crescent.

The Horses, by which term we include also Asses, Zebras and Quaggas, possess a dentition as complicated as that of any existing Mammals and perhaps the best way to elucidate the complexity of appearance in the teeth is to follow rapidly the stages in evolution of the dentition from the first appearance of the ancestral forerunner.

In the little Eohippus, or Dawn horse of Eocene times, an animal scarcely larger than a cat, we find that the incisors and canines are simple teeth and the premolars smaller and simpler than the molars which show no evidence of the involved pattern which they are later to assume. The upper molars possess the three cusps of the trigon with the addition of a hypocone and the first beginning of an ectoloph while the transverse ridges which appear later in phylogeny are foreshadowed by the presence of a small cuspule between each pair of cusps. The lower molars also are primitive teeth and, the paraconid being lost, display two pairs of cusps united by low transverse ridges.

In the later Eocene the last premolar only had taken on the molar pattern and the incisors were still simple cutting teeth. Before the end of this period the third premolar in addition had become molariform.

Lower Oligocene Horses show all the premolars molariform in appearance except the first; the upper incisors but not the lower exhibit a low enamel ridge behind the cutting edge, the first stage in the formation of what is now called the "mark."

The molars were still brachyodont. It must be remembered that in the Eocene the climate of Europe and North America was moist and subtropical and only during later ages did the elevation of the land and the consequently colder climate result in the formation of grassy plains. In the Miocene the forested swamp had given place in many districts to grassy plains and it is therefore in this period that we look for the development of high-crowned grazing molars instead of the brachyodont browsing cheek teeth universal among Mammals in earlier ages. In the middle Miocene we first find Horses possessing high-crowned teeth with coverings of cement such as are found in the Horses of today, but the milk dentition, lagging in progress behind the permanent teeth, still exhibits brachyodont molars. For some time during the Pliocene browsing Horses existed side by side with the more advanced grazing type but gradually became extinct and gave place to the latter more adapted form in which, however, the molars though distinctly foreshadowing the pattern exhibited by modern Horses, had by no means reached the present degree of hypsodonty.

The modern Horse (Fig. 78) possesses teeth which are extremely high crowned and have roots growing continuously until the animal is quite old. The dental formula is:

$$I \frac{3}{3}, C \frac{1}{1}, P \frac{4}{4}, M \frac{3}{3}, \text{total } 44.$$

In consequence of the length of the teeth the orbit has been pushed back beyond the tooth sockets and this results in a very elongated facial region. The first premolar, the "wolf" tooth, of each jaw is very small and functionless being lost early and the upper canines occur only in the male. The incisors are all stout teeth, the lowers somewhat procumbent, and meet in an edge to edge bite which, admirable for cropping grass, results in great and continuous wearing of the crown. In surveying the evolution of the equine

dentition it was stated that in the lower Oligocene the incisors began to exhibit a low enamel ridge behind the cutting edge. The development of this has resulted in the formation of a deep enamel ridge behind the cutting edge. The development of this has produced a deep enamel-lined pit, the "mark," on the

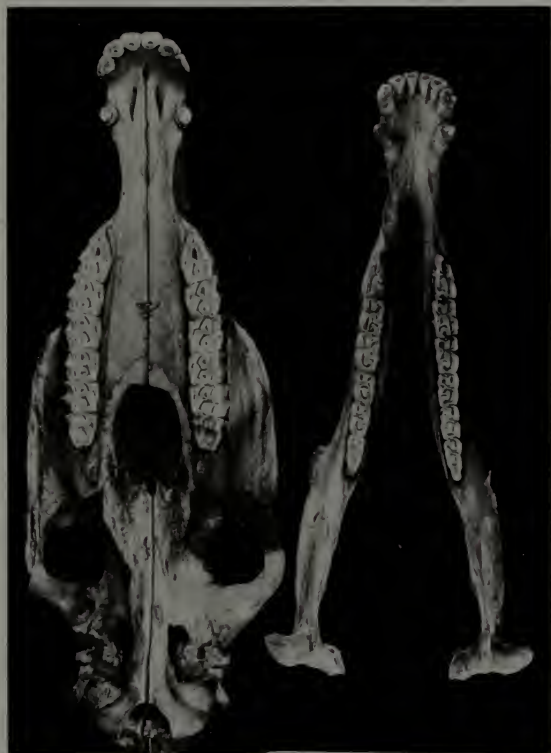


Fig. 78.—Dentition of Zebra (*Equus burchelli*, 9.725-1). This old male shows marked wearing of all the teeth. The upper canines are characteristic of the male. For the elucidation of the cusp pattern of the molars consult the text.

crown of the tooth, present in modern Horses in lower and upper incisors alike. As the tooth wears down this tube-like formation, since it never involves the entire crown, becomes less deep and in the old animal (see Fig. 78) only the last

remnant remains on the upper first and second incisors; upon all others there is a dark stain, the dental "star," an area of secondary dentine formed just in front of the line of the "mark."

Turning next to the cheek teeth, we note that all the functional premolars* are completely molariform in appearance, and the talonid of the last lower molar is elongated as usual in herbivorous forms. But the crowns of all the cheek teeth show an exceedingly complicated pattern. The teeth are hypsodont as would be anticipated but show extreme specialization of the occlusal surface. The crenated enamel ridges which in their highly complex arrangement can be seen even in worn teeth to be derived from the more primitive pattern of the teeth in *Eohippus* by the addition of styles, lophs and cingula which, if measured in all their closely packed infoldings, represent a length of about sixteen inches, that is four times the circumference of the tooth itself. Thus does Nature provide a surface upon which slight ledges of enamel, projecting beyond the dentine of the lophs themselves and the cement which occupies the spaces between the lophs, form roughenings always sharp and ready for the mastication of the relatively tough and hard grass stems upon which the animal feeds. It may seem a long way from the comparatively simple teeth of *Eohippus* to the intensely specialized teeth of the modern Horse with their maze-like pattern but we know from fossils practically every stage which intervened between them, and can assert positively that the complicated grinder of the modern Horse developed gradually in easy stages and by a slight modification at a time during the vast geological period which has intervened between the Eocene and the present day.

It is worth while then to pause a moment and look back into the paleontological history, not of the Horses alone, but of the Tapirs and Rhinoceroses also. We have already noted the fact that the *Perissodactyla* and *Artiodactyla* traced back to their earliest known ancestors still show such marked differences that

*The "wolf" teeth of the specimen figured were lost many years before death.

it is impossible to conceive their divergence from any common stock later than the very dawn of mammalian life. We have seen moreover that the Artiodactyla originated probably from a carnivorous stock, the creodont Mesonychidae. As we follow back the Horses, Rhinoceroses and Tapirs we find their Basal Eocene forerunners obviously related to each other and in addition we note close relationship between their ancestors and those of the Proboscidea and of Hyrax representing the two other Ungulate orders which we have still to discuss, and also with the ancestors of the Sirenia. It is probable then that all the orders just enumerated, with the exception of the Artiodactyla, trace their ancestry back to a group of Cretaceous Protungulata, clawed Mammals related to the Creodont-Insectivore stock, forest dwellers and possibly partly arboreal which in consequence of their mode of life escaped destruction by the then existing Dinosaurs and the known Cretaceous Mammals dwelling near the swamps or on the plains.

CHAPTER XIV

THE ELEPHANTS AND SEA COWS

Distribution of the Elephants—Characters of the Elephant dentition—Evolution of the Elephant—Features of the Sirenian dentition—Origin and relationships of the Sirenia.

PROBOSCIDEA

Five species of Elephant exist today, four of them in Africa and a single one in Asia but though the varieties and range of this animal are now greatly restricted, it was distributed in former times over the whole world except Australia, even penetrating into South America and was in consequence adapted for every kind of climate from subarctic to tropical. The Elephant gives striking confirmation of a general principle in mammalian structure, namely, that teeth and skull are much more progressive than the skeleton in general: Elephants of middle Miocene times are scarcely distinguishable in skeletal features from those of the present day although very marked changes have occurred in the dentition and skull.

To look at the example of young Indian Elephant figured (*Elephas maximus*, Fig. 79) one would wonder from what sort of ancestral form its teeth have been derived, for they are among the most specialized of all teeth, consisting as they do of a number of transverse plates of dentine coated on both sides with enamel and held together by cementum. Further in mode of eruption the Elephant molars differ from those of all other Mammals in that the successional tooth does not displace its predecessor vertically but erupts obliquely from behind and above in the maxilla, behind and below in the mandible.



Fig. 79.—Dentition of Indian Elephant (*Elephas maximus*, 9.614.1). This skull is that of a young female and shows the third molar in place in the jaws. The second molar is being pushed out of the maxilla.

The tusk is not a canine but a second upper incisor greatly elongated and procumbent, having only its tip enamel-covered

but its entire length coated with cement. There is a milk predecessor of this tooth but all other incisors, the canines and premolars both temporary and permanent are non-existent. There are three milk molars and three permanent molars in all but only one tooth is erupted at a time. Each succeeding tooth as it erupts pushes forward the worn remnant of the one in front causing it to be loosened and finally shed. In the specimen figured the third molar (corresponding to the first permanent tooth) is erupting and the insignificant roots of the second are being resorbed as the tooth becomes displaced. From the appearance of the teeth the Elephant is obviously a pure vegetable feeder, the Asiatic species living upon grasses, the African upon succulent boughs and foliage. The number of plates in the six successive molars of the Indian Elephant is: 4, 8, 12, 16, 24 to 27.

In the African Elephant the molars possess fewer plates, each less compressed but with occlusal edges mammillated when first erupted as in its Asiatic relative. To understand the mode of evolution of the molars it is necessary to refer to the extinct *Mastodon* in which we find not a very complicated hypsodont molar but a relatively simple brachyodont tooth in which the individual cusps have become united into transverse lophs. Intermediate in form between the molars of *Mastodon* and those of *Elephas* are the teeth of another extinct form *Stegodon* common in the upper Pliocene of India.

Earlier than *Mastodon* was a form living in Miocene times *Tetrabelodon* by name in which the molars were swine-like and though elongated showed cusps with commencing loph formation. At this stage the vertical succession normal for Mammals was still present.

Other and less advanced species have been found in the Oligocene and in the Upper Eocene of Egypt. In these (*Paleomastodon* and *Moeritherium*) the molars are simpler, less elongated and with the usual vertical replacement. In *Moeritherium* which existed from the Upper Eocene into the Oligocene the upper molars are fairly typical trituberculate teeth with the

addition of a hypocone and the lower molars present the usual tuberculo-sectorial structure with loss of the paraconid and elongation of the talonid. In each series the third molar has a pronounced posterior basal cingulum and it is from the constant growth and extension of this that the elongation of the tooth so pronounced in later races is brought about.

The Elephant molars are then no exception to the general method whereby adaptation of the tooth to an extreme browsing or grazing character is brought about. Indeed the molar does not strikingly differ from that of the Rodent *Capybara* and the same method of evolution of molars has already been studied in less pronounced form in the Pig, Bear, Baboon and Kangaroo.

SIRENIA

Closely related to the Proboscidea are the marine browsing Mammals, the Manatee of Florida and the Dugong of the Indian Ocean. These strange creatures also known as Sea-cows feed upon seaweed, eel-grass and aquatic plants.

The skull of the Dugong like that of the Elephant is markedly specialized and although the molars when first erupted show an occlusal surface of masked selenodont appearance this surface soon wears away and the teeth remain as simple hypsodont columns with permanently growing roots. In the upper jaw the incisors, apart from certain vestigial rudiments buried under a horny casing, are reduced to two long tusk-like teeth which in the female do not project beyond the gum (see Fig. 80) but in the male resemble Rodent incisors in that they possess persistently growing roots and have no enamel upon their posterior surfaces. In the mandible there are four or five rudimentary antemolar teeth on each side imbedded in the sloping surface of the symphysis which are functionless and are covered by a horny plate opposing the obliquely placed premaxillary part of the palate. Of the cheek teeth there are altogether five or six on each side with persistently growing roots all devoid of enamel and all cylindrical except the last which is elongated and grooved on

its inner and outer aspects. The anterior cheek teeth are lost as the posterior ones come into place so that only two molars remain on each side in older specimens.

It is obvious then that the Dugong has undergone reduction in number and functional capacity of the antemolar teeth. The Manatee on the other hand is a terminal form illustrating tooth differentiation of a quite different character: in it we see actual increase in the number of molars as we have already noted in



Fig. 80.—Dentition of Dugong (*Halicore australis*?, Oberlin College Collection). In this skull of an adult female note the reduced dentition, the simplified hypsodont cheek teeth and the site of rudimentary anterior teeth on the symphysis.

certain other highly specialized Mammals, the Armadillos and certain Cetacea for example. There is no doubt that such increase in number of molars may and does occur in mammalian orders though of the causes which bring it about we are completely ignorant.

In spite of the fact that the modern Sirenians are so very specialized we know enough of their ancestral history to state

that the forerunner of these animals was a terrestrial Mammal not very different from the Egyptian Eocene Ungulate *Moeritherium* the relationship of which to the ancestor of the Elephants has already been pointed out. We infer that this Oligocene predecessor early assumed an aquatic existence and that some members migrated from the Mediterranean to the Atlantic basin finally evolving into the Manatees while others entered the Indian Ocean to give origin to the Dugong. Why tooth reduction occurred finally in the latter and tooth increase in the former we do not know.

The number of genera of *Sirenia*, so far as we have evidence, was never very large but from such fossil forms as are known it is accepted that the primitive Ungulate ancestor of the order was a terrestrial, five toed, short legged animal with the usual primitive dental formula, brachydont bunodont molars, hinder premolars molariform, anterior ones simple, small canines and a tendency to the tusk-like elongation of one upper and one lower incisor on each side.

CHAPTER XV

THE HYRACES

Features of the Hyrax dentition—Similarity of its cheek teeth to those of Eocene Perissodaetyls—Relationships of Hyrax—Resemblances to Perissodaetyla and to Proboscidea—A Mammal retaining primitive features is not necessarily out of harmony with its environment.

These curious little animals (Fig. 81) from Africa and Asia Minor are somewhat of a zoological puzzle. They are of browsing habits feeding upon the leaves and young shoots of trees and bushes. The dental formula is:

$$I \frac{2}{2}, C \frac{0}{0}, P \frac{4}{4}, M \frac{3}{3}, \text{total } 36.$$

The large median upper incisors are triangular in section in the male, oval in the female, elongated and at first sight rodent-like in appearance. Like those of the Rodent they possess also persistently growing roots but the enamel is not confined to the anterior surface. The second upper incisors are tiny and very early lost. They are represented in the figured specimen merely by remnants of their alveoli. The lower incisors are rather procumbent, have persistently growing roots and present a comb-like appearance from elongation of the three tubercles which cap the crown. They occlude behind the upper incisors. After a short interval come the premolars all of which are molariform and increase in size from before backward whereas the molars present a decrease from before backwards. Comparison with Eohippus brings out a striking resemblance between the brachyodont* cheek teeth of Hyrax and those of

Eocene Perissodactyls. The upper molars present two obliquely placed lophs connecting protocone and paracone, metacone and hypocone respectively. In addition to these there is an ectoloph gathering up the two outer cones and the three primitive styles. Well-marked cingula are also present fore and aft. The last upper molar has no hypocone but instead the metacone has subdivided to produce a pseudohypocone in



Fig. 81.—Dentition of Hyrax (*Procavia brucei* var. *somalica*, 9.62-1). The example is an adult male. Note the rodent-like upper incisors. The characters of the cheek teeth at once preclude any relationship with Artiodactyl Ungulates.

the same manner as we have noted in herbivorous Marsupials (see page 85). A curious and interesting feature of the upper molars is their oblique setting in the maxilla so that a hinder

*The cheek teeth of the species figured are brachyodont, but from this it must not be inferred that the cheek teeth of all species of Hyrax are low-crowned. Progression to the hypsodont type has occurred in quite marked degree within the order and some species of Hyrax representing a more advanced form possess quite high-crowned cheek teeth. Further a hypsodont species is usually found living alongside a brachyodont species in the same locality just as in Miocene and lower Pliocene times species of Horses with high-crowned cheek teeth lived alongside less specialized brachyodont browsing forms.

tooth overlaps the one in front laterally as in the ruminant Artiodactyla. The lower cheek teeth present anterior and posterior crescents concave lingually but since the paraconid itself is absent the ridge passing forward and inward from the protoconid fades away at the anterior margin of the tooth. The hinder ridge of the anterior crescent passes from protoconid to the curiously reduplicated metaconid. The two ridges of the posterior crescent run from the hypoconid which forms the apex to the metaconid and entoconid respectively.

One peculiar and primitive feature of the skull is the extension of the malar into the glenoid fossa as in Marsupials. In spite of this Hyrax is obviously an Ungulate and its closest relationships might be suspected to lie with the Artiodactyls but this conception is immediately contradicted by many anatomical features. There is one of these which may be mentioned since emphasis has already been laid upon the essential and primitive differences between the premolars of Artiodactyla and those of Perissodactyla. The premolars are already very advanced in type and molariform in Eocene representatives of the order Hyracoidea. It may also be noted in passing that these early forms show an enlarged, pointed and triangular upper median incisor as in the existing Hyraces.

In many other features Hyrax resembles the remote Perissodactyla; in the reduplicated metaconid of the lower molars for example, a character exhibited also by the Eocene Megalohyrax. Nevertheless the resemblances of this animal to the Proboscidea in parts of the skeleton other than the teeth, considerably outweigh the significance of the Perissodactyl-like molars and premolars.

In short, as Dr. Gregory says, "the existence of so many 'cross resemblances' between the Proboscidea and Perissodactyla by way of Hyrax seems more consistent with the hypothesis that all these now very divergent orders have been derived from a common protungulate stock, than with the hypothesis that all the resemblances are due to convergent evolution."

Fascinating though the Hyrax may be in its anatomical fea-

tures and zoological relationship we must not occupy more space over the animal. But it is well to point out that although like the Tapir it may with some justice be nicknamed a "living fossil" because it bears in its body so many primitive features unchanged or only very slightly modified during its long ancestry, yet it is by no means an antiquated animal in the sense that it is out of touch with its environment. The Tapir indeed is naturally stupid and uninteresting; that may be because we have little interest in the lines along which the Tapir's intelligence moves. The Hyrax on the other hand is intensely active, easily tamed and learns with rapidity, having a natural bent as it were for investigation and experimentation. Perhaps the most charming part of Dr. Chalmers Mitchell's delightful book *The Childhood of Animals* is that wherein he tells of the activities and learning powers of his pet Hyrax. One of the basal necessities of life for every animal is that it should be able to adapt itself to its environment.

CHAPTER XVI

THE BATS

General position of the order—Megachiroptera and Microchiroptera—*Vespertilio fuscus*—Importance of the incisor specialization—Molars of the Fruit Bats.

The Chiroptera or Bats possess a very long history having been highly specialized even in Eocene times. Their anatomy however reveals the probability that they originated from primitive arboreal Insectivores perhaps of the Cretaceous, perhaps of the Basal Eocene. Their dental formula is derived by reduction from the primitive Placental type. There are two groups of Bats, the Megachiroptera or Fruit Bats and the Microchiroptera or insectivorous Bats, the latter being the more specialized in their general anatomy. But just as the Walrus though generally less specialized than the Seals yet has a dentition more aberrant, so also the Fruit Bats generally less removed than the insectivorous Bats from typical Insectivores, present a dentition in which it is much more difficult to trace homologies. The link connecting the Fruit Bats with the Insectivores proper is the so-called Flying Lemur, *Galeopithecus*.

For the purpose of this volume it will be sufficient to glance at the dentition of one of the Microchiroptera, the more specialized group. We have therefore figured the skull of the common Brown Bat, *Vespertilio fuscus* (Fig. 82). The number of incisors and cheek teeth differs greatly among the Bats but in *V. fuscus* the formula is:

$$I \frac{2}{3}, C \frac{1}{1}, P + M \frac{4}{5}, \text{total } 32.$$

The upper median incisors are separated by a wide gap and the lateral ones are pointed teeth. The lower incisors are small, semi-procumbent and their crowns are each surmounted by three globular tubercles. The canines both upper and lower are long and sharp. The distal three cheek teeth in both jaws are molari-form and but little removed from the general Insectivore type. Each upper member, except the last, presents a trigon with the three typical cusps and three styles and in addition a low hypocone. The protocone being reduced, the other cusps of the

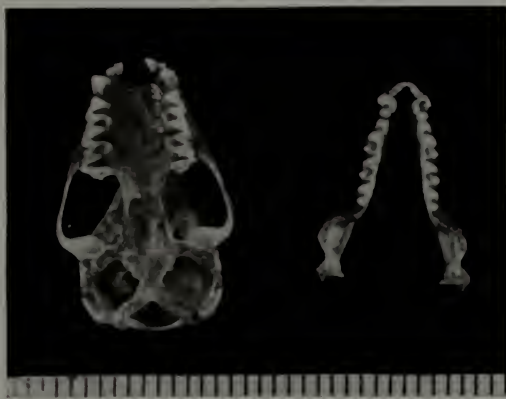


Fig. 82.—Dentition of Brown Bat (*Vespertilio fuscus*, 9.4-1). Note the typical Insectivore molars and the very specialized incisors.

trigon and the styles give a prominent W-appearance to the occlusal surface. The last molar has its posterior moiety mutilated. On each of the three last lower cheek teeth is a typical trigonid with three cusps and a large talonid with hypoconid and entoconid. All the cusps are long, sharp and needle-like as usual in insectivorous teeth and the more anterior post-canines simple and conical. The premolar-molar series resembles that of the Mole very closely in the characters of the individual teeth.

In the above description it is worthy of note that the molars are not so specialized as the incisors. In discussing the denti-

tion of the various orders of Mammals it is almost impossible, because of their greater complexity of form, to avoid seeming to lay especial emphasis upon the molars. The student is therefore apt to gain the impression that adaptations of these teeth are the most if not the only important changes to be observed in the dentition. If he will pause for a moment to consider the infinite variation in mammalian incisors and to think of the very different modifications required for seizing or gathering according to the particular food habit of the animal, the reader will readily realize the enormous importance, as emphasized by Bensley, of incisor modifications in determining the morphological characters of the entire dentition. Perhaps this significance of the incisors is most plainly seen in the Marsupials among modern Mammals. We have been able to treat of the Marsupials at greater length than other orders because of the large number of representative stages in evolution of teeth still in existence. Such instances as the Horses and the Rodents will however present themselves at once as marked examples of adaptation of incisors in association with great modification in the dentition as a whole.

Finally lest any reader, observing the peculiar molars of the Fruit Bats, should wonder how these can fit in with the view put forward at the beginning of this chapter it must be stated that there is evidence to show that, though greatly specialized, these have undoubtedly been derived from the typical mammalian tritubercular tuberculo-sectorial type.

CHAPTER XVII

THE WHALES AND PORPOISES

Whalebone Whales and toothed Whales—Evolution of the dentition in the toothed Whales—Ancestry of the Whales—Dentition of the Porpoise.

Of the Cetacea there are two suborders, one the *Mystacoceti* or whalebone Whales, very highly specialized and possessing instead of teeth large masses of whalebone hanging from the roof of the mouth; the other the *Odontoceti* or toothed Whales having simple peg-like teeth sometimes in great number. Whereas the former group feeds upon small shrimp-like crustaceans and swimming molluscs the latter is carnivorous in habit. With the *Mystacoceti* we shall not deal in this volume although minute vestigial two- and three-rooted teeth have been described as existing in whalebone Whales prior to birth, but shall devote our attention solely to the toothed Whales with which are associated the Porpoises and Dolphins.

These animals though possessing teeth are in many respects even more specialized and aberrant than the *Mystacoceti* and it is probable that the two are parallel groups possessing a common ancestor but diverging from each other during their phylogenetic history. The simple peg-like tooth armament or to speak in scientific terms, the haplodont, homodont dentition of the *Odontoceti* is not primitive as might at first appear but is derived secondarily from the more typical tritubercular tuberculo-sectorial form. This secondary simplification is an adaptation to aquatic carnivorous feeding and is seen in a less advanced stage in the Sea-lions and Seals. In the toothed Whales as well as in the Pinnipedia there is very great varia-

tion in the form of the teeth which is itself evidence of the comparatively recent differentiation of the dentition. But this does not mean that the Odontoceti and the Pinnipedia are related. It simply indicates that similar habits call forth a similar adaptation though in varying degree. In other words the similar secondary simplification of the teeth in these two suborders is one of convergent evolution. We have seen that the Pinnipedia are probably related to the Miocene "Bear dogs" but although the Odontoceti are also carnivorous they are certainly not related to any known carnivorous Mammals.



Fig. 83.—Dentition of common Porpoise (*Phocaena communis*, 9.53-1). Note the great number of similar cylindrical teeth and the extreme specialization of skull and jaws.

There may have been typical Odontocetes in the Oligocene but it is quite possible that the Whales are of more recent origin. There is nothing in their anatomy to suggest great antiquity as for example in the cases of the Edentata and the Rodentia. The derivation of all the Whales, toothed and toothless, seems to be from Insectivore-Creodont stock but the earliest examples at present known are certain fossils from the middle Eocene of Egypt, *Protocetus* and *Mesocetus* by name, primitive creatures which, while perhaps not representing the direct ancestral stock, are at least collateral to it.

The example which we have chosen to represent the toothed Whales is the common Porpoise, *Phocaena communis*, the diet of which consists exclusively of fish. Inspection of Fig. 83 shows that the jaws are long and relatively weak and that the teeth are small, similar, very numerous, with spade-like crowns and constricted necks. The enamel organs are not much developed and the teeth consist of a special type of dentine with a coating of cement. Some *Odontocetes* possess very few teeth and some, like the Dolphin, more than twice as many as the Porpoise figured.

The great number of similar cylindrical teeth of the toothed Whales is only approached in certain *Armadillos* in which the teeth lack enamel entirely and are the result of a much more ancient specialization. It is in the toothed Whales that we see secondary increase of cheek teeth at its maximum.

CHAPTER XVIII

THE MONOTREMES

Extreme antiquity and specialization of both existing families—The Spiny Anteater—Food habits and dentition of the Duck-billed Platypus—No evidence of close relationship between existing Monotremes and Multituberculata.

Since one of the existing Monotremes, the Spiny Anteater of Australia and New Guinea is entirely toothless like the placental Anteaters and Pangolins, and since the other, the Duck-billed Platypus of Australia and Tasmania has teeth which are merely transitory, this order is not of great significance for our immediate purpose.

Many archaic and reptilian features are retained in the anatomy of these animals but nothing is known of their actual fossil history which must therefore be inferred from the study of modern forms alone. The characters of the shoulder girdle indicate that Monotremes originated from very early Mammals not far beyond the reptilian stage and certainly before the diverging marsupio-placental forerunners had begun to adopt an arboreal existence. During the lengthy period since their origin, very marked peculiarities have appeared in both animals which must therefore be considered separately from even the primitive marsupio-placental stock. Certain bodily features however occur in both Spiny Anteater and Duck-bill which in addition to the geographical distribution of the animals indicate a common if very remote ancestry for the Monotremes and Marsupials. Beyond this we cannot proceed until further evidence is available.

Ignoring then the edentulous Spiny Anteater the skull and

jaws of which show the same modifications consequent upon entire loss of teeth as do those of the Anteaters already discussed, we turn our attention to the transient dentition of *Ornithorhynchus*.

This fossorial semi-aquatic animal possesses peculiar jaws armed in the adult not with teeth but with horny thickenings of the epithelium. For crushing the shells of fresh-water molluscs upon which the animal feeds teeth would be poor and brittle instruments. On the other hand the nutcracker-like

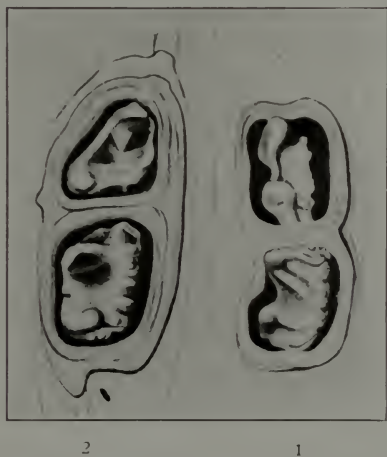


Fig. 84.—Dentition of Duck-billed Platypus (*Ornithorhynchus anatinus*, enlarged, after Oldfield Thomas). 1, left upper teeth. 2, left lower teeth. The third tooth is not represented; the first is very aberrant but in the second may be traced indications of an originally tritubercular tuberculo-sectorial type.

jaws with their horny covering are excellently adapted for grinding such food. Notwithstanding the fact that there are no teeth in the adult, actual teeth corresponding to the permanent dentition of other Mammals and even vestiges of a deciduous dentition have been discovered. The “permanent” teeth are three on each side of each jaw, twelve in all and after great attrition from which they are worn to the thickness of paper they are shed when the animal is about two-thirds grown.

The two anterior teeth are large but the third very small

and all are obviously cheek teeth. Fig. 84 reveals the fact that although little can be made out concerning the first tooth the second presents in masked form the general characters of the tritubercular tuberculo-sectorial type. (The third is not shown.) The upper tooth possesses a trigon the large protocone of which is connected by ridges with paracone and metacone and in addition there is a well-developed hypocone. The outer border of this tooth like the inner margin of the corresponding lower molar is complicated by numerous small secondary tubercles. The second lower molar presents a paraconid and an elevated protoconid though the metaconid and the entoconid are obscure. The heel on the other hand, shows a large hypoconid. The teeth are much broader than high and their vestigial roots penetrate the underlying growing horny layer to reach the bone in which however they are not deeply imbedded.

Misled by the tuberculate appearance of the teeth, some authors have likened them to those of the Triassic Multituberculate Marsupial *Microlestes*. The similarity in appearance between these two is merely superficial. The tooth structure in *Ornithorhynchus* is profoundly different from that in *Microlestes*. On the ground that the Monotremes represent the lowest phase of mammalian life other writers have sought to find in the teeth of *Ornithorhynchus* indications of what must have been the dentition of the early Mammals. This is plainly a false trail for an animal so aberrant and specialized with an ancestral history reaching back to the very dawn of mammalian life, and especially of such peculiar feeding habits as *Ornithorhynchus* could not be expected to retain teeth at all approximating in appearance the typical ancestral mammalian form. There is then no great difficulty in accepting for the teeth of this animal a tritubercular tuberculo-sectorial origin.

CHAPTER XIX

THE DECIDUOUS DENTITION

Specialized Character of the monophyodont dentition in Mammals—The deciduous teeth do not represent in miniature the permanent teeth—Milk Dentition of Modern Man—The Předmost mandible—Milk dentition of Anthropoids—Deciduous dentition of Old-World and American Monkeys—Mingled ancestral and adaptive features of the deciduous dentition—The milk dentition in orders other than Primates—The Marsupial dentition—Foramina of the tooth crypts.

There is no doubt that Mammals were originally derived from Reptiles possessing a polyphyodont dentition, one in which there occurred many successional series of teeth. Replacement of teeth is known to have occurred in Cynodonts and in Jurassic Mammalia. It is therefore natural that the less specialized of modern Mammals at least should exhibit two series, the temporary, deciduous, lacteal or milk set and the replacing, successional, or permanent set. When we find Mammals which possess only one functional series of teeth such for example as the Seals,* Sloths, toothed Whales and many Rodents, we must regard the feature as evidence of great specialization. This interpretation is borne out by the fact that it is usually in those members of any order more advanced in other respects which exhibit the so-called monophyodont character. Consequently we consider that Mammals which have retained a complete milk dentition consisting of incisors, canines and milk molars,

*The milk dentition of the Seals is shed before birth.

the last being the predecessors of the premolars, are the less specialized and exhibit what is truly an ancestral feature.

In many respects the milk dentition differs from the permanent set in the characters of its constituent teeth, not so greatly perhaps in the incisors, but more in the canines and most of all in the milk molars, often called milk premolars, the last of which at least is of a pattern much more closely resembling the molar teeth of the successional set than the premolars. From this fact two widely different interpretations have been drawn, one that the milk series represents the ancestral characters of the dentition such as were possessed also by the permanent set in earlier forerunners, the other that the milk teeth are specialized for the peculiar needs of the young animal. Both of these views present elements of truth and we shall therefore examine them with some attention.

It can scarcely be said that the diet of young Mammals, once they are beyond the stage of suckling, differs materially from that of their parents so that the 'particular needs' of the immature animal are not directly connected with the type of food. It is however common knowledge that the facial skeleton of the young animal, in contradistinction to that of the adult, is relatively small in proportion to the size of the skull as a whole, and this for reasons beyond the scope of our present inquiry. In the childhood of all Mammalia the jaws are comparatively short and the teeth themselves are absolutely, though not necessarily, relatively smaller than in the adult. Indeed it can be demonstrated readily in any series of animals with a well-developed milk dentition, let us say the Anthropoid Apes, avoiding as far as possible racial discrepancies, that the incisors tend to be relatively smaller and the molars relatively larger in the milk dentition than in the permanent. Sex distinctions in the canines again are not so pronounced in the milk dentition and the teeth themselves are small. The same divergences can be observed equally well in Man and for them there must be some adequate explanation. In another section (page 268) we note that within limits those teeth nearest to the at-

tachment areas of the masticatory muscles and to the fulcrum, that is to say to the temporo-mandibular articulation, are the teeth in the best situation for exerting pressure and are molariform whereas those teeth furthest removed from muscle attachments and joint are best placed for swift movement and cutting or piercing action and are simple chisel-like (incisors) or conical (canines) in shape. Intermediate in position are the premolars which are also intermediate in function.* In the milk dentition the relative shortness of the jaws is associated with fewer teeth: those forms of teeth naturally are found which are most essential to the animal's existence. Hence the milk postcanines in Man and the Anthropoids reproduce the more fundamental features of the cheek teeth *as a series* in the permanent dentition.

This suggestion calls at once for study of the milk teeth that we may find out what are the more essential features of the human and Anthropoid dentitions. It brings home to us the fact that neither of the terms milk molars and milk premolars accurately defines the characters of the deciduous postcanine teeth.

The milk dentition of Man, of all Anthropoids and Old-World Apes is:

$$i \frac{2}{2}, c \frac{1}{1}, m \frac{2}{2}, \text{ total } 20.$$

We shall take as our first example the milk dentition of the European (Figs. 85, 86).

Apart from smallness of size the deciduous teeth possess enamel of a different hue from that of the permanent teeth. The neck is relatively better marked, the crown being more globular and in the case of the molars the roots more divergent than in the successional teeth. As to the incisors which are quite vertically situated in the jaws the relationship in size

*This interpretation must not be expected to fit all facts. For example in the very specialized Horse the premolars are all completely molariform in appearance though their relation to muscular attachments and joint is not closer than in Mammals with less complex premolars.

between central and lateral teeth, both in maxilla and mandible, is about the same as in the second dentition.

The first obvious difference is seen in the canine which is globular as already stated, has a very convex outer aspect and projects if anything slightly more beyond the occlusal surface of the rest of the teeth than in the adult dentition. The first postcanine in both jaws is a peculiar tooth. Though somewhat

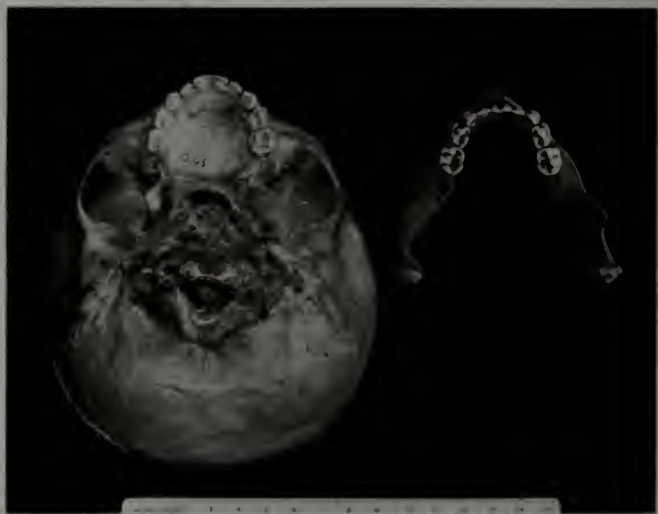


Fig. 85.—Deciduous dentition of modern European (0.95, W.R.U.). Note that except in the case of the incisors the teeth do not represent in miniature the teeth of the adult dentition (Fig. 53).

molariform it does not present the definite molar characters of the second and is plainly specialized for the purpose of acting as a link between the simple incisors and canines in front and the complex grinder behind. The upper tooth presents outer and inner cusps as in the permanent premolars but its outer cusp is very broad and elongated antero-posteriorly by connected styles so that the crown is triangular in shape. The crown of the lower tooth possesses anterior and posterior moieties, the latter shaped and presenting cusps like the talonid of

a molar. The anterior moiety is much narrower, being beveled at the expense of its labial portion and shows two cusps in the sites of the protoconid and metaconid together with a ledge in front which probably may represent the paraconid or at least a protoconid-paraconid shear. The two cusps on the



Fig. 86.—Right lateral aspect of child's skull sculptured to show roots of temporary teeth and crowns of developing permanent teeth. (After Dewey-Thompson.) Note the constricted necks of all teeth and the curved roots of the molars between which the replacing teeth are developing.

tafonid are probably homologous with the hypoconid and entoconid of the permanent molars. The second postcanine tooth is much more like a permanent molar, is indeed often said to duplicate the first permanent molar in miniature but this is

not exactly true. In both jaws the second milk molar has an occlusal surface relatively narrow compared with the crown because of the marked beveling of the latter upon its outer side. The maxillary tooth is neither so rhomboidal nor so obliquely set in the jaw as the corresponding first permanent molar. It possesses a very large protocone and relatively small paracone and metacone, the oblique ridge between the latter and the first mentioned being present as in the permanent molars. The hypocone is small though distinct. The crown of the lower tooth is relatively very long, the lateral grooves between the cusps are deep and the cusps well separated: the talonid is broader than the trigonid. The protoconid and hypoconid are small and the metaconid very large so that the cross furrows so typical of the permanent molars do not exist. The entoconid is of moderate size and the hypoconulid not axial but lateral in position.

If now the features just described be compared with those of the permanent molars already interpreted in Chapter VII, it will be seen at once that they form a curious mixture of ancestral and specialized characters. Whereas the features of the second upper milk molar and the arrangement of cusps (except the hypoconulid) of the lower second may well be considered primitive, the reduction in size of the occlusal surface from that of the crown proper and the lateral position of the hypoconulid cannot be so regarded. Hence the disproportionate length of the occlusal surface of the second lower molar is secondary in origin. The interpretation of the first premolar is not so simple and must be deferred for the moment.

When we turn to the milk dentition of the modern Negro we find that the description given above for the temporary teeth of the European holds fairly well and there is no need for special description.

In Paleolithic types we have not many examples of milk teeth, but from the accompanying figure of the mandible of a child about seven years old discovered in an upper Paleo-

lithic burial site at Předmost in Moravia (Fig. 87), we learn that the lower first milk molar was less molariform and the second possessed an occlusal surface approaching more nearly in breadth the crown itself while the hypoconulid was more axial in position than is the case today. We cannot say that the Předmost mandible is of unmixed strain. Though probably of primitive *Homo sapiens* stock there may be in it some admixture of Neandertaloid blood. However this may be the mandible indicates to us the increasingly specialized condition of the modern milk dentition.



Fig. 87.—Mandibular dentition of Paleolithic European from Předmost. (After Walkhoff.) A less specialized milk dentition than that of today. The teeth present are the first and second deciduous molars and the first permanent molar.

We must now examine the deciduous teeth of the Anthropoids (Figs. 88-91) and note if we can obtain from these some indication of what our milk dentition used to be. In doing this it is essential that we should bear in mind the early divergence of the human and Anthropoid lines. Whereas our own ancestors early became cursorial and predaceous and therefore developed a tendency rather toward a carnivorous and later a grain diet, the Anthropoids, especially the Orang, progressed toward a completely frugivorous diet.

As in the case of Man we will pass over the incisors with the simple statement that in the Anthropoids also we find these

teeth more vertically placed than in the adult, obviously a surviving ancestral character. The canines more triangular in the Chimpanzee and Gibbon than in ourselves are more pointed in the Gorilla and the Orang. The first upper milk molar is bicuspid and plainly triangular in the Gibbon and Gorilla but shows a tendency to antero-posterior extension of the palatal cusp in the other two great Anthropoids. The first lower milk molar presents a large pointed cusp with a tiny subsidiary one on its lingual aspect and a low and ill-developed

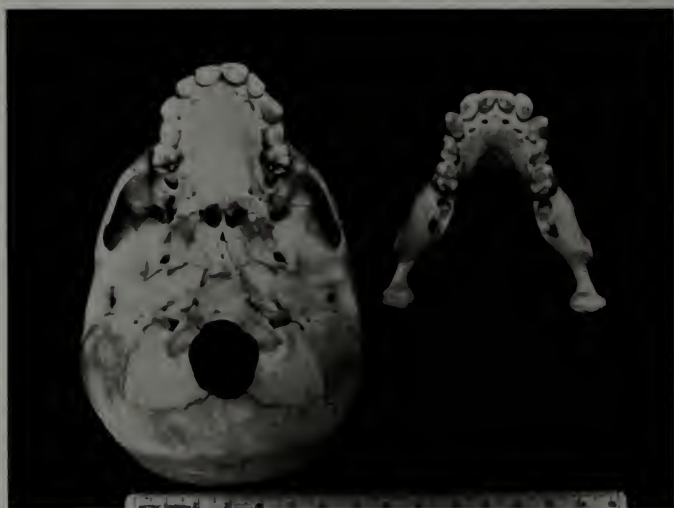


Fig. 88.—Deciduous dentition of Chimpanzee (*Pan* sp., 9.88-11).

heel behind in the Gibbon, Gorilla and Orang but in the Chimpanzee this tooth approximates the human form, resembles indeed the *Předmost* type somewhat for the inner cusp is larger and the heel is well developed and presents two cusps as in ourselves (Fig. 88). The second upper molar is a typical tritubercular tooth with a hypocone in all Anthropoids but in the Chimpanzee and Orang the cusps are low and even indefinite and secondary crenations appear as in Man. The second lower molar in the Gibbon presents primitive Anthropoid characters.

Its occlusal surface is long and as broad as the crown. The metaconid and hypoconid are large and the hypoconulid axial in position. The same description holds for the Gorilla in which the metaconid is very large. In the Chimpanzee the occlusal surface becomes restricted transversely and the hypoconulid migrates somewhat laterally, so that it is not unlike the second lower molar of the *Předmost* mandible. In the Orang the pinched-in condition of the occlusal surface is very



Fig. 89.—Deciduous dentition of Gorilla (*Gorilla* sp., 9.88-12).

pronounced though the hypoconulid remains more axially situated than in man. The molars resemble quite considerably the lower *first* milk molar of the human dentition, a case of convergent evolution in which the terminal appearance has been brought about in very different manner in the two cases. The forms of the two upper milk molars and the lower second are comparatively easily understood. With regard to the lower first molar it seems that in the Anthropoids with tusk-

like canines this tooth somewhat resembles in function the lower canine since it also forms a shear with the upper canine. In the Chimpanzee on the other hand and still more in Man the canines are reduced and the first lower milk molar possesses an ever increasing tendency to become molariform.

From this brief review and from what we know of the history of the human milk dentition we may conclude that considerable specialization has occurred in the human milk molars,



Fig. 90.—Deciduous dentition of Orang (*Pongo pygmaeus*, Hoppius; 9.88-7).

especially in the first, adapting them to the needs of the organism, and further that analogous specialization can be observed in differing degrees in the Anthropoid Apes according to their requirements, the specialization affecting the several teeth in varying measure. But in spite of the superposed adaptive features, quite pronounced though they may be, certain primitive and ancestral characters are not entirely overshadowed.

As was stated at the beginning of this chapter two views are held regarding the milk dentition, first that it represents features possessed also in ancestral forms by the permanent set and secondly that it displays specializations for the requirements of the young animal. We now see that these views are not mutually contradictory but each is true so far as it goes.

The term "milk molar" as appears from the foregoing description is no more adequate than the name "milk premolar"



Fig. 91.—Deciduous dentition of Gibbon (*Hylobates concolor*, Harlan; 9.88-4). The first molars, central incisors and right lower lateral incisor of the permanent set have erupted and may readily be distinguished by their white color.

to express in a word the characters of the deciduous cheek teeth. We have noted in earlier chapters that in the permanent dentition the premolars cannot always be distinguished clearly from the molars by their appearance. Nor can we define the premolars as possessing forerunners while the molars do not, for in most instances there is no tooth preceding the first premolar of the permanent set (see Fig. 93). According to

M. F. Woodward this condition is brought about by the presence of a large canine which, occupying so much space in the jaw, results in a deformed permanent first premolar and leaves no room for a corresponding milk tooth. This view seems to be borne out by the cases of the Hyrax and the Tapir (see Fig. 77) in both of which the first premolar possesses a predecessor. In the former animal the canine is vestigial and never becomes a functional tooth, in the latter it is reduced and separated by a considerable distance from the premolar series.

As for eruption of the deciduous teeth it is well known that the lower central incisors are the first to come into place in the jaw. When one recalls that in the act of sucking the maternal nipple is compressed between tongue and palate, the lower jaw serving merely to steady the tongue, it becomes evident that these teeth can erupt without causing irritation or damage to the delicate skin of the nipple and so enable the mother to continue suckling her infant for a longer time than would be possible otherwise. It is also clear that as the young animal grows and the jaws lengthen there will be unoccupied space behind the second milk molar. This provides a site for the developing first molar which is thus the earliest of the permanent teeth to come into position.

The deciduous dentition of both Old- and New-World Monkeys affords confirmation of the conclusion attained above that the milk teeth do not resemble in miniature any of the permanent set.

In some Old-World Monkeys, *Pithecus rhesus* for example (Fig. 92), the differentiation of the first milk postcanine in both jaws has proceeded to a much more molariform stage than in the Anthropoids generally. The upper tooth is quadricuspid from the appearance of a hypcone and although the trigonid of the lower tooth is relatively narrow the talonid is comparatively better developed than even in Man. The second milk postcanine is more completely a replica of the first permanent molar than in the Anthropoids or in ourselves, a condi-

tion to be expected from the more molariform condition of the first milk molar.

Passing to the New-World Monkeys we find a somewhat different state of affairs. These animals possess three permanent premolars and three milk molars but the first successional tooth to erupt, as in the various Old-World families, is the first molar. In the Sapajou Monkey (*Cebus*) which we may take as an ex-



Fig. 92.—Deciduous dentition of Bengal Macaque (*Pithecus rhesus*, Audebert; 9,823-11). In this animal the milk teeth have approached more closely in feature to the permanent teeth than in Man or Anthropoids.

ample the milk incisors and canines, though small, do not show such striking divergences from the patterns of the corresponding permanent teeth as do the postcanines. There being one more postcanine than in the Old-World families the essential functions of shearing and crushing can be more distributed. Consequently while the last milk tooth is purely molariform the first is equally definitely sectorial and of simple premolariform pattern, the tooth which is intermediate in position being

also intermediate in appearance. The lower first postcanine exhibits merely a cingulum, no heel; the second has a crown approximating in appearance but by no means reproducing the features of its successional premolar; the molariform third is longer and narrower with a relatively larger trigonid and smaller talonid than the first permanent molar. Analogous differences exist in the upper teeth. The first has only a low cingular cusp on the palatal side of the apex; in the second which is elongated transversely this palatal cusp has increased in size and prominence; in the third it forms a rounded protocone, the main cusp (paracone) is replaced by a reduplicated one (paracone and metacone) and there is developed a small hypocone. We note then that close resemblances between milk teeth and their successors are accidental in nature and more to be wondered at than striking differences.*

When we turn our attention to other animals, we again constantly find evidence of mingled ancestral and adaptive features in the milk dentition. In the Aye-aye for example the milk teeth are much less specialized than the permanent set and clearly indicate by their more primitive features the lemuroid character of the animal. In its milk dentition the Horse possesses shorter crowned teeth with characters simpler than those of their complex, hypsodont, permanent successors. In the milk dentition of the Dog (Fig. 93) there are three postcanines of which the first upper and first and second lower are simple premolariform teeth, the second upper and the third lower sectorial and the third upper molariform, thus reproducing in miniature the essential features of the adult dentition *as a whole*.

In carnivorous animals generally the milk teeth play their part and are shed early. In the Seal they are shed before birth. In some animals, the Edentates, for example, the milk dentition is quite vestigial but such teeth as there are show much less specialization than their permanent successors. The milk

*The gradual increase in complexity of the milk molars backwards representing as it were stages in development culminating in the pattern of the first permanent molar is very striking in the New-World Monkeys. The reader is referred in this connection to statements made on pp. 62, 103 regarding the Premolar Analogy Theory.

dentition is heterodont, whereas the permanent teeth are homodont. In the toothed Whales the milk teeth are entirely vestigial. Herbivorous feeders on the other hand retain at least some of their milk teeth until they are sufficiently adult themselves to give birth to young and this is probably an adaptation to save the permanent teeth in view of the extreme attrition to which, in consequence of the nature of the food, the dentition of these animals is subjected.



Fig. 93.--Deciduous dentition of Dog (*Canis familiaris*, 9.7424-47). The milk dentition as a whole reproduces the features of the permanent dentition as a whole. The large simple tooth erupting immediately behind each canine is the first premolar of the permanent set, a tooth which in most animals does not possess a predecessor (but see Tapir, Fig. 77).

According to some authors there are evidences of as many as five dentitions among Mammalia, one before the milk teeth, one after the permanent set and another antecedent to the premilk series. This last rests, it must be admitted, upon very slender evidence. Dr. Ameghino is responsible for the statement that in a long extinct Ungulate, *Nesodon*, there were developed three successive dentitions of which the second and third correspond with the modern milk and permanent series respectively. The same author asserted that at least one func-

tional premilk premolar occurs in the Tapir. Although this seems to be a uniquely surviving feature of the ancient mammalian dentition it is of scarcely sufficient importance in the present connection for treatment at length.

Earlier in this chapter the statement has been made that usually it is the more advanced species of an order which have lost their milk dentition. This is not invariably the case. The Rat for example, by no means the advanced of Rodents, possesses so far as we know at present not even a vestige of temporary teeth. On the other hand the two very specialized Marsupials, *Myrmecobius*, the Banded Anteater and *Phascinomys*, the Wombat, both possess clear evidence of a definite milk dentition whereas in the less aberrant Marsupials the milk dentition is still more vestigial since only a single lacteal tooth persists.

This brings us to the consideration of Marsupial teeth in general. We have noted previously some of the many curious specialized and aberrant features of this order and in consequence it is not surprising to learn that only one tooth is replaced in these animals. During the discussion of the marsupial dentition this has already been noted and reference should be made to Chapter IV for details. That one tooth only should be replaced is no new feature of the dentition since the Jurassic Marsupial, *Triconodon*, shows the same phenomenon. A very striking feature of the case is the fact that in the modern Marsupials as in *Triconodon* it is the same tooth, the forerunner of the last premolar, which is replaced in all species. Whereas in most other tooth changes in Mammals the succeeding tooth develops rather behind the tooth which it replaces, in this instance the successional tooth develops somewhat in front of its predecessor.

Opinion at first favored the view that the functional dentition of the Marsupials in general represented the permanent set. Later views inclined toward homology with the milk dentition. Recently however the former conclusion in modified form is becoming more generally accepted and the evidence grows clearer that the Marsupials of today are specialized in their

dentition to the extent that there is, with the exception of the two animals above mentioned, no functional remnant of the milk teeth unless it be this replaced tooth. The question which immediately presents itself is the true nature of the so-called deciduous tooth replaced by the last premolar. Tims has upheld that it is really the first of the permanent molars which becomes projected above the last premolar in consequence of a progressively relative shortening of the palate in relation to its breadth as the animal grows older. He maintains that a similar explanation holds in the case of the Dog and the Guinea-pig in which animals the last permanent premolar also is very unlike its forerunner somewhat in front of which it develops. Tims claims that his ingeniously presented theory covers the case of certain Insectivores in which, however, the successional tooth does resemble its forerunner. It is stated that the replacing tooth in Marsupials is not embryonically connected with either of the teeth between which it develops and which it succeeds. On this account it cannot be the homologue of either. Even after reading carefully Dr. Tims' statements and considering the evidence he presents I cannot see that his conception clears the situation and while his view may be correct it is not entirely satisfying at present. There is nothing unusual in a successional tooth being of different appearance from its actual predecessor. Examples of this have been cited from many mammalian orders. We have already noted the special adaptations exhibited in the milk molars both of Man and of the Anthropoids. We have observed moreover that the milk incisors and canines are comparatively small teeth, their successors relatively large. The developing permanent successors of these teeth must then lie rather lateral and posterior to their predecessors in the jaw. It is only when we come to the premolar region that we find the actually smaller teeth which take up less room in the jaw succeeding the larger milk molars. A change in relative position between the deciduous teeth and their successors is therefore to be expected in this area. The successional premolar in the Marsupials is not

cramped for space in the jaw but it is a very large and specialized tooth modified for sectorial purposes and as such may be expected to cause some disturbance in the dentition as it erupts in such animals as the Kangaroos. The question of relationship in appearance and position of the last permanent premolar to its predecessor and the special difficulties regarding tooth replacement in the Marsupials must therefore be left *sub judice*.

One last feature of the temporary dentition must be mentioned. The milk teeth always lie to the outer or labial side of their successors even in the case of the molars, although the developing permanent premolars project between the divergent roots of their predecessors. If the student examine the carefully cleaned jaws of any young Mammal (see for example the infant Chimpanzee, Fig. 88), he will note foramina in the bone upon the lingual or palatal aspect of the milk teeth, one immediately behind or internal to each tooth, those related to the incisors and canines being large, those near the milk molars small and overhung by the corresponding tooth. These are the openings in the bone through which passed the dental rudiments of the permanent teeth and at the bottom of each hole is the crypt containing the corresponding successional tooth. Since these foramina are of necessity absolutely invariable their presence indicates with certainty that the erupted tooth adjacent to each belongs to the deciduous series. The absence of the foramen gives equal assurance that the corresponding tooth is of a member of the permanent set.

CHAPTER XX

THE ROOTS OF TEETH

Evolutionary importance of the roots—Paleotelic and caenotelic Characters—Features of the root in mammalian teeth—Nature's methods of combating attrition—Inferences from the deep-seated position of the canine root in Man—The roots of teeth in Man and Anthropoids—Specialized roots of teeth in the Aye-aye—Roots of teeth in Neandertal Man.

During his perusal of the foregoing chapters the reader must have been impressed by the fact that practically the entire discussion has related to modifications of the cusps and crowns of teeth. He will have observed the wide range of adaptation of the cheek teeth to changes in habit and the profound bearing upon the whole dentition of the form of the incisors but he is justified in asking why roots have received such scant mention. It will of course be quite evident that the exposed crowns from their very position must command attention whereas the roots buried in the jaws are less accessible. Nevertheless it is equally apparent that study of the roots must have its importance in adequate consideration of the dentition as a whole. It might even be argued that the roots are at least as important as the crowns because of the fact that being imbedded in the jaws they are less influenced than the crowns by modifications of environment. That they are not entirely unaffected by environmental changes is sufficiently indicated however by the frequent transformation in many orders of the brachyodont into the hypsodont type of tooth.

In this connection the student should understand the difference between *paleotelic* and *caenotelic* characters. These terms

were coined by Gregory to take the place of the words *morphological* and *adaptive* respectively. A paleotelic or morphological feature is primitive and unaffected or but slightly modified by external conditions. Examples are the auditory ossicles, the foramina of the skull, certain features of the base of the skull, the carpal and tarsal bones and the urogenital system in general. In all of these there is but restricted variation except in certain special types. On the other hand some features such as the facial skeleton, the fingers and toes, the color of the skin and the character of the hair vary through a considerable range in consequence of their exposure to environmental conditions. Such characters are caenotelic and not primitive, but greatly modified. Should, however, a paleotelic feature become exposed to environmental influence as in the case of the auditory ossicles in aquatic Mammalia it becomes greatly modified and thus caenotelic in nature. Now upon this basis the crowns of the teeth, being as a rule much more influenced by external conditions than the roots are likely to show greater changes. In other words their paleotelic characters are more likely to become obscured. Infinite are the variations of cuspidation but strikingly few and slight are the modifications of the roots of teeth.

No biological "Law" is really an explanation. It is in essence a description of sequences. We are not explaining why changes occur in structure when we state more or less vaguely that they occur in part at least in response to environmental influence: we are but correlating facts. When we state that certain changes in structure appear apparently as the result of modification in external conditions we are giving an instance of what may be termed the Law of Environmental Influence. Returning then to the subject of teeth it may be stated that the paleotelic characters of the crowns have become largely obscured whereas those of the roots show greater tendency to persist. For this reason the tooth crown has received considerable attention in this volume and the root but little.

One feature wherein the mammalian dentition differs from

that of Reptiles is the possession of teeth with more than one root. It is not true of all mammalian teeth and is more characteristic of the molars than of the antemolar series. In the Cynodonts we find the reptilian character of a single root even in the flat quadrate molars of *Sesamodon* and the very mammal-like molars of *Diademodon*. The cheek teeth of Protodonta show incomplete separation of the root into two fangs (Fig. 13). In all known Triconodonta and Trituberculata on the other hand the premolars and molars present at least two roots. In the upper teeth these support the para- and metacones respectively but in some genera, *Dryolestes* for example, the upper molars differ from the premolars in possessing three roots, a large medial one beneath the protocone and two smaller lateral ones supporting the outer cusps of the crown. In most primitive Mammals likewise, whether they are of marsupial or placental stock, the premolars and molars are two-rooted although the protocone and its supporting internal root in the upper molars may be absent. We are justified then in considering the two-rooted brachyodont type as the primitive mammalian form. Further, it is by no means uncommon to find an actual bifanged appearance in the canine. This condition occurs in *Talpa* the Mole, and in *Erinaceus* the Hedgehog, both being animals which from their lowly ordinal position are likely to retain unchanged the primitive features of the tooth roots. On reference to Fig. 94 it will be noted that evidence of separation of the root into two exists even in the incisors of certain primitive animals.* Grooving of the root of a tooth must then be taken as indicating a geologically older bifanged condition.

We have observed previously that there are various ways whereby the teeth become elongated to compensate for marked attrition, the result of a herbivorous diet. There is the elongation of the cusps so well seen in all lophodont Marsupials especially in the grazing Kangaroos, and the elongation of the body of the tooth so plainly marked in the Bandicoot *Thala-*

*The Flying Lemur *Galeopithecus* has two roots in the outermost (third) incisor as well as in the canine.

comys. In both of these types the roots are fully completed in the adult teeth and do not grow persistently as in the case of the Horse which represents a much more advanced stage. Again attrition is compensated for in a totally different manner by forcing up of the stump of the worn tooth so that the last possible wear can be obtained even after the crown is practically nonexistent. This condition also is well illustrated in the Horse. All three methods are manifested in conjunction though in differing degrees by many Mammals.

While progression toward complete hypsodonty is usually associated with increase in complexity of crown pattern this is not invariably the case. Among the extinct Ungulates peculiar to South America there lived during the Pleistocene a stoutly built semi-aquatic lumbering animal named *Toxodon*.

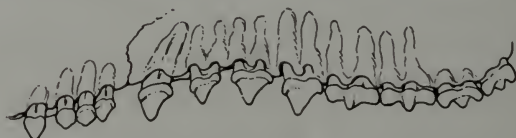


Fig. 94.—Upper teeth of Jerboa Pouched Mouse (*Antechinomys laniger*, after Gregory). As in all primitive Mammals the canines, premolars and molars possess two large external roots.

Further back and separated from *Toxodon* by a vast geological period there existed in the Miocene a smaller and lighter beast *Nesodon* which we have already mentioned because of a peculiarity in its dentition (page 253). It is probable that *Nesodon* is actually the ancestor or at any rate very closely related to the ancestor of *Toxodon*. The molars of both animals were hypsodont but the curious fact is that the crowns in *Nesodon* were decidedly more complex than those of its descendant *Toxodon*. We must then be always upon the watch for exceptions to general rules which we find it necessary to formulate.

In a typical specialized hypsodont Ungulate the cusps are observed to be long but a more striking feature is the loss of distinction between crown and root. The neck of the tooth does not exist. Further the root, if one may term it such, is

obviously single but not primitively so: rather it represents the fused roots of the primitive tooth uncompleted at the apex. In the Horse it is only in old age that the divergent root tips appear. Completely hypsodont teeth possess roots of persistent growth and such have already been observed in advanced forms of incisors and molars alike.

It is especially striking that in the Horse which is an example of extreme hypsodonty the milk dentition even today is less high-crowned, thus confirming the view just put forward that the brachyodont type with two or more roots is primitive.

From lack of space it is impossible to deal adequately with the tooth roots in all orders but a little attention to the appearances found in the higher Apes and in Man will not be misplaced.

The first feature which strikes the observer in comparing the teeth of an Anthropoid with those of Man is the fact that each of the upper premolars possesses three roots like the molars. Three roots are occasionally found in the human upper premolars; in fact I am inclined to believe that this condition is not so rare as is said to be the case. The bifid or three-pointed tip and the grooving of the root are indications of a former separation into more than one fang. Both in Anthropoids and in Man grooving of the root of the canine and of the incisors occurs, in the former more frequently than in the latter. These features and in addition the clearly marked separate roots of non-persistent growth so characteristic of all Primate teeth with one exception are certain evidence of the retention of fairly primitive root features in this order.

The skiagram of a jaw in which the permanent teeth are still developing focuses attention upon the situation of the canine rudiment. This lies much more remote from the gum than any of the other rudiments (see Fig. 86). In the great Anthropoids we have already noted that date of eruption of the canine varies with sex. In the female Chimpanzee it erupts before the third molar but in the male it is the last tooth to come into place. In both cases the canine erupts

relatively much later than in Man in whom, however, it lies just as deeply imbedded as in the Anthropoids. No sexual distinction in time of eruption of the canine has been noted in the human dentition yet the deeply seated position of the rudiment of this tooth is a sure indication that it was formerly powerful and long-rooted as in the Anthropoids today.

In both Anthropoids and Man the root tips of the second and third mandibular molars lie near the inferior dental canal



Fig. 95.—Skiagram of jaws of Chimpanzee (*Pan* sp., 9.88-16). In this adolescent female the canine has erupted before the third molar. Note the very close relation between the developing roots of the third molar and the inferior dental canal which opens out (unlike the condition in Man, Fig. 96) into a large space at the level of the second molar. In the adult Anthropoid the root tips of the third molar even overshoot the inferior dental canal.

but in the former they often overshoot the canal itself, a condition not found in Man in whom from the tendency, very obvious in modern Europeans, toward shortness of root the root tips are further removed from the canal than they are in Anthropoids (Figs. 95, 96). The precise distance naturally varies with the individual. In the Heidelberg mandible there is a very

close relationship between the root tips and the canal as one would expect from the primitive nature of this jaw. The relative shortness of the roots in human teeth is the precise opposite of the condition found in the Orang for the extreme length of the tooth roots of which no adequate explanation has yet been offered. If now we examine a skiagram of the jaws of the Aye-aye we note once again shortness of the roots especially



Fig. 96.—Skiagram of jaws of Negro (Skull 524, W.R.U.). The molar roots are relatively long in this case and approximate the inferior dental canal almost as in the Anthropoid. This is not so in all human mandibles.

in the second and third molars when we compare these with the teeth of other nearly related Lemurs (Fig. 97). We note further that associated with the shortness of roots is the lack of a well-defined neck. In Heidelberg Man there is also a practical absence of the tooth neck. The Aye-aye is a marked exception to the retention in Primates of a relatively primitive type of tooth. It is a significant exception because the features of its cheek teeth assist us to realize what is happening in the

case of the human dentition. We must therefore consider the matter in a little more detail.

Not only do the cheek teeth of the Aye-aye possess relatively short roots fused in part of their extent, but this fusion, least marked in the first molar, involves progressively more of the roots in the second and most in the third. This is natural since, as we have frequently observed, it is the first molar which is the most stable. Again the pulp chamber of all three



Fig. 97.—Skiagram of jaws of Aye-aye (*Daubentonia madagascariensis*, 9.815-1). Note the short roots fused in part of their length especially in the third molar, and the large pulp chamber the outline of which sinks beneath the level of the alveolar border of the jaw.

molars but more especially of the third is relatively long and tends to sink beneath the level of the alveolar border of the jaw.* This is a marked distinction from the appearance pre-

*It is true that the pulp chamber diminishes in size with age through the appearance of secondary dentine, and that in consequence the skiagram of the jaws of a young animal will show a larger pulp chamber in the third molar than in the first, because the latter erupted long before the former. Any fallacy in interpretation of Fig. 97 upon this score is precluded by the fact that the specimen is an old one. The interpretation given is further indicated correct by the progressive fusion of the roots backward in the molar series.

sented by all other Lemurs including the Indrisinae which are the nearest relatives of the Aye-aye. In other Lemurs as in the Anthropoids and in most types of Man the pulp chamber is shallow and clearly defined and its outline lies entirely without the alveolar border. Long narrow root canals alone appear in the tooth below the level of the bone surface. In those instances of modern Man in which the molar roots are short and exhibit a tendency to fusion we find as in the Aye-aye a less clearly defined outline for the pulp chamber which is long and extends beneath the alveolar border. Many Neandertal teeth, it is true, exhibit features differing little if at all from those



Fig. 98.—Teeth of Jersey Neandertal Man (after Keith and Knowles). Upper row: upper teeth: 1. third molar, 2. first right molar, 3. second left premolar, 4. second left molar, 5. third left molar. Lower row: lower teeth: 1. third right molar (crown), 2. second right molar, 3. second right incisor, 4. left canine, 5. first left premolar, 6. second left premolar, 7. second left molar. This is a form of Man with extremely specialized tooth roots. Note the short fused molar roots, the absence of neck and the great attrition of the crown.

which are characteristic of most modern dentitions but some skulls (Fig. 98) present features of very different type. Not only are the molar roots short and fused into a solid mass but the neck of the tooth is lacking, the crown merging with the stump-like root, and the pulp chamber is large, long, imperfectly outlined and extends far below the alveolar border. Even the root canals are capacious and form simply loculi of the elongated pulp chamber. This thoroughly distinctive appearance, indications of which are met with in some modern

skulls, is comparable with the similar condition displayed by the molars of the Aye-aye. It has been defined by Keith as the *taurodont* type, because it considerably resembles the hypsodont character of the Ox molars in contradistinction to the *cynodont* appearance presented by the vast majority of modern human molars which are more primitive in feature and in skiagrams display characters of the pulp chamber and roots somewhat similar to those of the Dog. The specialized characters found so much more frequently in Neandertal than in modern molars are so striking and so unlike the typical human dentition that they create an impression fast becoming a conviction in the minds of many anatomists that Neandertal Man cannot have been an ancestor of our own line but was rather a specialized and now extinct offshoot of the human race.

We believe that the food of Neandertal Man was not purely carnivorous but included tough vegetables and grain. In addition these ancient people were probably not averse to the chewing of hides a habit indulged in today by the Eskimos in whom be it noted the taurodont form of molar tends to appear more frequently perhaps than in any other modern race. The specialized diet of the Aye-aye has been discussed in Chapter VI. It is impossible to avoid the impression that the teeth of Neandertal Man and those of the Aye-aye represent degrees of the same modification brought about under the influence of dietary habit. The reader must remember of course that not all Neandertalers exhibited this peculiarity. This fact, the relatively infrequent occurrence of the condition in modern Man and the total absence of the modification in Anthropoids leads us to believe that the taurodont form of molar is a progressive feature of the Primate dentition. In this character therefore Neandertal Man had progressed far beyond the stage which we ourselves have attained, had in fact reached a position approached among Primates only by the very aberrant Lemur *Daubentonina*.

CHAPTER XXI

THE EVOLUTION OF TYPES

Biological interpretations and laws—External and internal factors inducing variation—Examples of pronounced divergence within a single family—Theories of modifications in dentition—Migration of teeth in the jaw—Variations and mutations once more—Creative Evolution.

Having now completed our brief survey of mammalian teeth, we turn our attention to certain features of the dentition as a whole which, though deeply interesting, are until now imperfectly understood. It has already been emphatically declared that a truly satisfying explanation of phenomena is not given by a statement of sequences nor does one answer the question *how* by making an adequate reply to the question *why*. In all so-called biological interpretations and in all biological laws one must be on one's guard against confusing these two simple interrogatives *how* and *why*. We have seen that differences in life habits, especially differences in diet, are associated with changes in tooth form and we infer that the former at least in part called forth the latter. But if this be a true statement of fact it does not throw any light on how the changes are brought about. One may wonder if the alterations in tooth form are compelled by some dominating force of which we are ignorant or if perhaps they are mere chance variations pounced upon and utilized by natural selection.

— Every dental student knows that individual variations occur in all the teeth yet the complete dentition of any individual, broadly speaking, is true to type. We have observed that the dentition may differ considerably from species to species.

Some for example have brachyodont molars, others hypsodont, yet each species though living side by side with the other breeds true.

We have noted the fact that different genera within a single family show strikingly how completely dissimilar one dentition may be from another. We have also seen that traced back to their simplest or earliest representatives the dentitions of most if not all mammalian orders indicate derivation from a common forerunner. In mentioning one external factor which assists in bringing about modifications in the dentition, namely diet, we have merely opened the question of the origin of modifications. We have made no suggestion of a possible force inherent within the organism tending to bring about alterations. To the problem, unsolved as yet, of how changes are produced we have devoted no attention whatever. One cannot leave the subject of teeth without at least glancing at these enigmas of how and why. Many problems of modern biology have found or will find their solution in experimental investigation, a field closed to us in the study of teeth. So far as dentition is concerned we can but observe the imperfect record of Nature's experiments carried on over vast periods of geological time.

Early in our inquiry it was noted that the conformation and articulation of the jaws underwent great modification in the transition from Reptile to Mammal and at the same time the homodont dentition gave place to the heterodont. It has been suggested that the cheek teeth being close to the joint and to areas of direct muscular pull are best situated for crushing or shearing whereas the incisors and canines, further removed, operate through a larger arc with greater velocity and are hence in a position to execute cutting and piercing functions. It is true that in many animals the transition between the simple cutting incisiform and the larger crushing molariform type is gradual and progressive through canine and premolars but in the Horse and the Hyrax, to mention only two examples, the transition is abrupt. It cannot be doubted that such sudden transition is secondary in view of its non-occurrence in an-

cestral forms, nevertheless the abrupt change must have become stereotyped very early since we find it present in the *Cynodonts*.* The relation of teeth to jaws, to musculature and to the temporo-mandibular joint must be regarded as one factor only of those responsible for bringing about existing modifications of the several tooth forms. The very fact that we see in all orders of Mammals a definite tendency on the part of the dentition to evolve along one or another of certain well-defined lines itself suggests an internal heritable factor.

The teeth of the modern Tapir are practically indistinguishable from those of its Miocene forerunner yet we cannot say why this animal has undergone no change during so vast a period in which other animals, the Horse and the Whales for example, have developed striking dental modifications.

We have dealt fairly comprehensively with the varied forms of teeth represented today in the single order Marsupialia and have noted that some members retain quite primitive forms of teeth although in others the dentition is highly specialized. Emphasis has been laid upon food habits as a factor responsible for these differences but food habits alone have not produced the change. Had we taken any series, the Bandicoot family for example, and studied the varying forms of teeth exhibited by these animals whose food habits differ little if at all, we should still have noted progressive modifications which in the Bandicoots culminate in the most specialized form *Thalacomys*.

Instead of dilating upon this theme at wearisome length in the chapter on the Marsupials a further consideration of these progressive changes of less degree has been postponed until the student should be better acquainted with the end results, as it were, of Nature's experiments. We are now in a position to appreciate the importance of these gradually progressive changes. We might lay out in order of succession a series of examples of any family or even genus taken from different geological epochs and, comparing them, note the ever changing

*The abrupt change from simple incisiform to crushing molariform teeth is to be found even in certain fishes.

forms of the teeth. We should observe that the change has always been in some definite direction toward final forms which are approximately the same as the latest example of series drawn from other orders. Starting with the insectivorous-omnivorous type the lines of progression are toward the long or short jawed pure Carnivore or in another direction through the omnivorous form, either to one of several varieties of pure herbivorous feeder (Ungulate) or to the highly specialized gnawing type (advanced Rodent). The student will have recognized that the fundamental plan of progressive evolution in teeth is common to all mammalian orders.

We are studying in this volume the dentition of modern Mammals, not of fossil forms and hence we do not propose to carry out the suggestion put forward in the preceding paragraph, but shall examine existing members of the order Carnivora in which we may observe the self-same facts. Why some genera have retained primitive tooth forms and others, closely related, have not, we are scarcely in position to state. We can only say that external conditions call forth a response on the part of the organism which is always along one of several clearly defined directions.

Instances cannot be multiplied on account of lack of space: we will give only two examples, one from the Civets, the other from the Raccoons, illustrating progression in form of teeth within a single family.

Fig. 99 contains photographs of the skulls of four Viverridae; namely the Rasse, African Civet, Fossa and Binturong. The formula of all is

$$I \frac{3}{3}, C \frac{1}{1}, P \frac{4}{4}, M \frac{2}{2} \text{ (Fossa } \frac{1}{0} \text{), total 40 (34).}$$

Apparent exceptions to this formula are produced in the Fossa since the first premolar of each jaw in this animal is shed in early life, and again in the Binturong in which the mandibular first premolar is lost in youth. The habits of all these

animals except the Rasse are little known though the Binturong differs from the others in being more thoroughly omnivorous, even including fruit in its dietary. The differences in palate and in tooth form are very striking. The Rasse and the African Civet are long jawed; the other two, in each of which the first premolar is shed in early life, are short jawed. The insectivorous character of the teeth of the Rasse is indicated by their sharp cusps; the carnivorous tendency by the carnassial form of $\frac{P_4}{M_1}$. The carnassial development is greatest in the Fossa, the jaws and teeth of which closely resemble those of the Cats. In the African Civet on the other hand the teeth and jaws simulate those of the Dog. We shall not stay to discuss these resemblances in detail: they are sufficiently obvious upon careful examination of the photographs and are approximate recapitulations in another family of the general method of tooth differentiation found in the true Cats and true Dogs. It is perfectly plain also that the dentition of the Binturong originated from a Rasse-like form, now considerably modified: the crowns are small and the cusps greatly reduced, a typical retrograde character which may be seen also in the dentition of the Kinkajou (Fig. 100).

The other example chosen (Fig. 100) does not show divergent modifications as have been noted in the feline- and canine-like Viverridae just presented. It illustrates the evolution of a single form of dentition, that of the Raccoon, showing as nearly as possible the stages met with in ancestral fossil Raccoons, reproduced in existing and closely related animals. It presents further the evolution of a retrogressive type, the Kinkajou, comparable with the Binturong. Lastly it exemplifies a very strange development, the formation of a pure herbivorous dentition from one originally carnivorous. This is all the more impressive when we recall the fact that modern Artiodactyla are descended in all probability from carnivorous forms, the Creodont family Mesonychidae. The simplest type



A

Fig. 99-A. Dentition modifications in the Viverridae. Indian Rasse (*Viverra malaccensis*, 9.7422-3).



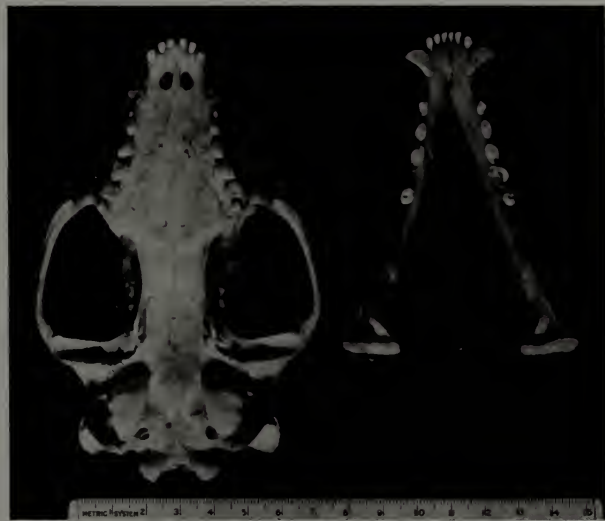
B

Fig. 99-B.—Dentition modifications in the Viverridae. African Civet (*Viverra africana*, 9.7422-2).
For explanation see text.



C

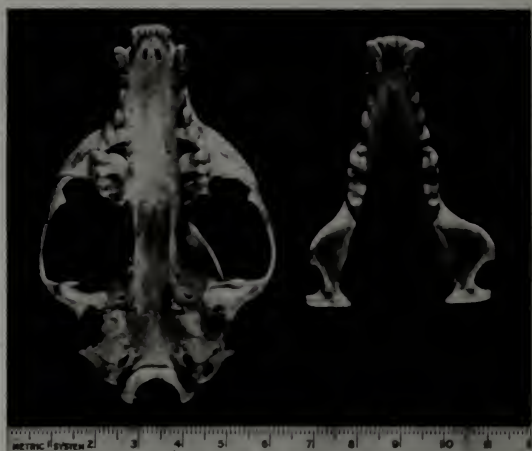
Fig. 99.C.—Dentition modifications in the Viverridae. Fossa (*Cryptoprocta ferox*, 9.7422.4).



D

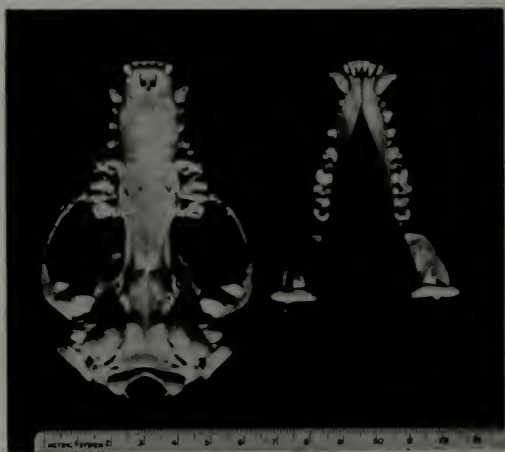
Fig. 99.D.—Dentition modifications in the Viverridae. Binturong (*Arctictis binturong*, 9.7422.5).

For explanation see text.



A

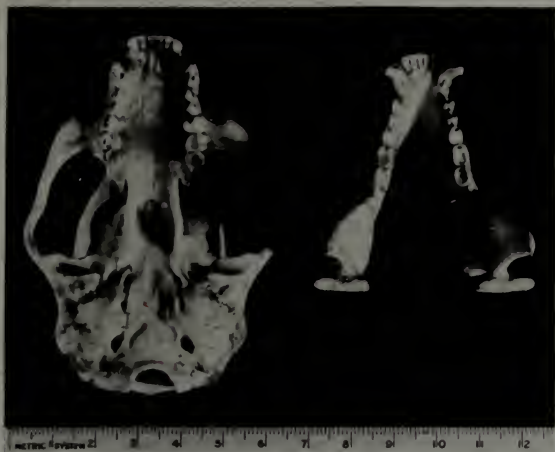
Fig. 100-A.—Dentition modifications in the Procyonidae. Cacomistle (*Basaris astuta*, 9,7425-7).



B

Fig. 100-B.—Dentition modifications in the Procyonidae. Raccoon (*Procyon cancrivorus*, 9,7425-3).

For explanation see text. In series between A and B is the dentition of the Coati-mundi (*Nasua narica*, Fig. 64).



C

Fig. 100-C.—Dentition modifications in the Procyonidae. Kinkajou (*Potos caudivulus*, 9.7425-6).



D

Fig. 100-D.—Dentition modifications in the Procyonidae. Fanda (*Aelurus fulgens*, 9.7425-5).

of dentition is seen in the *Cacomistle*, a more progressive form in the *Coati* (Fig. 64) and the fully developed condition in the *Raccoon*. Some details regarding the dental features of these animals have already been given in the chapter upon the *Carnivora* (page 182). The formula for each is:

$$I \frac{3}{3}, C \frac{1}{1}, P \frac{4}{4}, M \frac{2}{2}, \text{total } 40.$$

From this formula the dentition of the *Kinkajou* and the *Panda* are also derived but the former has lost the first pre-molar in each jaw and the latter has lost its maxillary first pre-molar and sheds the corresponding mandibular tooth in early life. The diet of these animals is increasingly omnivorous in the order *Cacomistle*, *Coati*, *Raccoon*. The diet of the *Kinkajou* includes flesh but consists largely of eggs and fruit and the teeth of this animal though clearly derived from a *Cacomistle*-like form are quite retrogressive; the carnassial teeth, well marked in the *Cacomistle*, are no longer specialized. The diet of the *Panda* is composed of fruits, eggs, acorns, roots and the young shoots of bamboos. The animal will not touch flesh. The photograph of the *Panda* should be examined with the greatest care for the student can easily identify therein the various cusps and styles and can observe the transformation of an insectivorous-carnivorous type of dentition into a purely herbivorous brachyodont type tending toward the selenodont form. The initial formation of the crescents, concave laterally in the maxilla and convex laterally in the mandible can be studied exceedingly well.

The foregoing are among the most instructive examples of tooth variation to be found in modern Mammals. In the photographs it will be seen that considering the marked differences in the teeth the condyles and glenoid fossae are remarkably similar. It would seem as though changes in the form of teeth long antedate structural modifications of masticatory significance in the jaws. However this may be it directs our attention to

the various attempts made to explain *how* changes in dentition have been brought about. Ryder, Cope and Osborn have successively attacked this problem but the real significance of an internal factor in the organism itself dawned only upon the last mentioned.

Ryder's view was that modifications in type of mastication result in changes in tooth form. He pointed out that there are different degrees of lateral movement in mastication in Ungulates; none at all in the Pig, slight movement only in the Wart Hog, movement progressively greater in the Tapir, Deer, Camel and Ox in this order. Ryder also pointed out that in Ruminants the food is masticated on the side of the mouth on which the lower molars cross the uppers from within outward (ental form), whereas in Horses and Rhinoceroses it is upon the side on which the lowers cross the uppers from without inward (ectal form). In the Rodentia the movement of the mandible on the upper jaw is antero-posterior (proal form). Ryder believed that the selenodont forms of Ungulate teeth are mechanically produced as the result of the direction and extent of excursion of the mandible in mastication.

Cope elaborated Ryder's interpretation and deduced certain mechanical causes as operating to bring about dental modifications. The operation of these supposed mechanical causes with their resultant effect upon the organism, Cope termed Kinetogenesis. We have already seen that modifications of tooth forms are apt to precede changes in the type of the temporo-mandibular articulation so that we cannot accept Ryder's interpretation. We shall see immediately that it is not possible to agree with Cope's theory of Kinetogenesis either.

In considering Cope's theory Osborn's attention was drawn to the fact that those areas of tooth crowns most subject to wear are precisely those which in subsequent geological types develop new cusps. Upon a purely mechanical basis this can only mean an increasing resistance leading to actual growth of tissue, the exact opposite of Cope's view according to which there is diminished resistance leading to plastic moulding of the

occlusal surface. At present one cannot conceive of the inheritance of an acquired* character: that an individual should transmit to its progeny dental features which it exhibits as the result of wear is utterly at variance with all known principles of heredity. The tooth, it must be remembered, is pre-formed in the jaw and its enamel-covered crown cannot grow or change actively in response to conditions of occlusion. Again the tooth is not firmly fixed in the bone: it is capable of considerable change in position. That teeth do move is obvious from the wearing which occurs upon the proximal and distal aspects of the molars. The exceedingly loose manner in which the incisors of the Cow are imbedded in the mandible has previously been noted. The alteration in level of a tooth in consequence of damage to or loss of its opponents is well known. The raising and loosening of a molar, the occlusal face of which is worn down or carious is especially manifest immediately after it is crowned by the dentist. At this time the tooth can be "wobbled" between the fingers but in the course of a few weeks during which the patient will notice the resilience of the tooth in its bed of softer tissue before the bony socket again grasps its roots closely, becomes firmly imbedded once again.

The change in position of teeth in the jaws in some animals is very well marked. We have already stated that replacement of teeth in all Mammals except the Proboscidea is vertical; in these animals alone it is oblique. We must now modify this statement somewhat. As a molar of the Elephant erupts, it moves forward in the jaw and hence changes its position with respect to the bone. It is not immovably fixed in the jaw as if it were imbedded in a matrix of Portland cement. When we come to examine more minutely the jaws of Mammals in which replacement is vertical we find many instances of the same forward movement of teeth even resulting in the shed-

*The term is a poor one. Archdall Reid pointed out some years ago that all characters can be said to be the result of interaction between internal potentiality and external stimulus. Nevertheless the precise sense in which the term is used in the present instance is sufficiently explained by the latter part of the sentence.

ding of the most anterior members of the series. In Hyrax there is to be observed the beginning of this forward movement. At first the anterior cheek teeth are more crowded together so that the total extent of occlusal surface of the entire series becomes less as the animal grows older. Finally the crushed and worn anterior teeth are shed to give room for the more recently erupted permanent ones. The same process on a more pronounced scale is seen in the Kangaroo, the Manatee and other Mammals. The Wart Hog is a conspicuous example. When the permanent teeth first erupt the dentition is almost the same as that of the Pig, certain important teeth being absent. The formula is:

$$I \frac{1}{3}, C \frac{1}{1}, P \frac{3}{2}, M \frac{3}{3}, \text{total } 34.$$

The third molar equals in antero-posterior length the entire series of cheek teeth in front of it. As they become worn down, all these anterior teeth are shed one by one, the last molar alone occupying their place and the formula becoming:

$$I \frac{1}{3}, C \frac{1}{1}, M \frac{1}{1}, \text{total } 16.$$

We have already seen that molars undergo striking differences in appearance in advance of equally extensive changes in the temporo-mandibular joint. Further we have noted that similar parallel or convergent types of tooth form develop independently in many orders. On all these grounds, therefore, we must reject not only the hypothesis that teeth are modified in response to changes in the mode of mastication but also the whole mechanical theory of Kinetogenesis as applied to tooth forms. We cannot resist the conclusion that modifications in dentition are in part the expression of heritable constitutional factors concerning which we know nothing as yet.

Now this brings us once more to the difference between

a variation and a mutation, definitions of both of which have been given upon page 31. Each individual of every generation in all species shows innumerable mutations throughout its body. Some of these are without significance upon the life of the organism; some are distinctly detrimental and under the operation of the Law of Natural Selection will result ultimately in the extinction of the type; others again bring the individual more closely into harmony with its environment and this in turn results in the dominance of the type, perhaps ultimately to the exclusion of other types, as for example in the paleontological history of the Horse. But, it may be objected, the evolution of hypsodonty in the Hyrax has not resulted so far in extinction of the brachyodont species although hypsodont forms have been present ever since the Miocene. This we cannot explain. Hypsodont and brachyodont species of Hyrax exist together under what are apparently the same conditions in the same locality. We must admit that there are controlling the modification of tooth forms factors of which we are utterly ignorant.

We now find ourselves in the domain of philosophy arguing against the mechanical interpretation of things. One of the tenets of Bergson's doctrine of Creative Evolution is that there is a constant progression in life, the evolution of new features. Nowhere in the body is this doctrine more strikingly exemplified than in the teeth which are among the most progressive of bodily structures and nowhere is the inadequacy of a mere mechanistic interpretation more obviously unsatisfactory. To quote Darbishire reflecting Bergson's metaphor: "A rolling stone gathers no moss. That is because a stone is a lifeless thing. But a living thing whose life is made up of its experience is like a snowball which is rolled in the snow; it increases, as it is rolled, with the snow that it gathers, until it is big enough to make a snow-man of. * * * When we look at life we are in the presence of the continual creation of the absolutely new." It is not to be expected that a single mutation appearing in a single individual is ever going to be able to

change the form of the whole race but the same or closely similar mutations appearing at the same time in a host of individuals, it may be of various species within a genus, can and certainly do result in the origination of a new type less or equally or more in harmony with the ever changing environment.

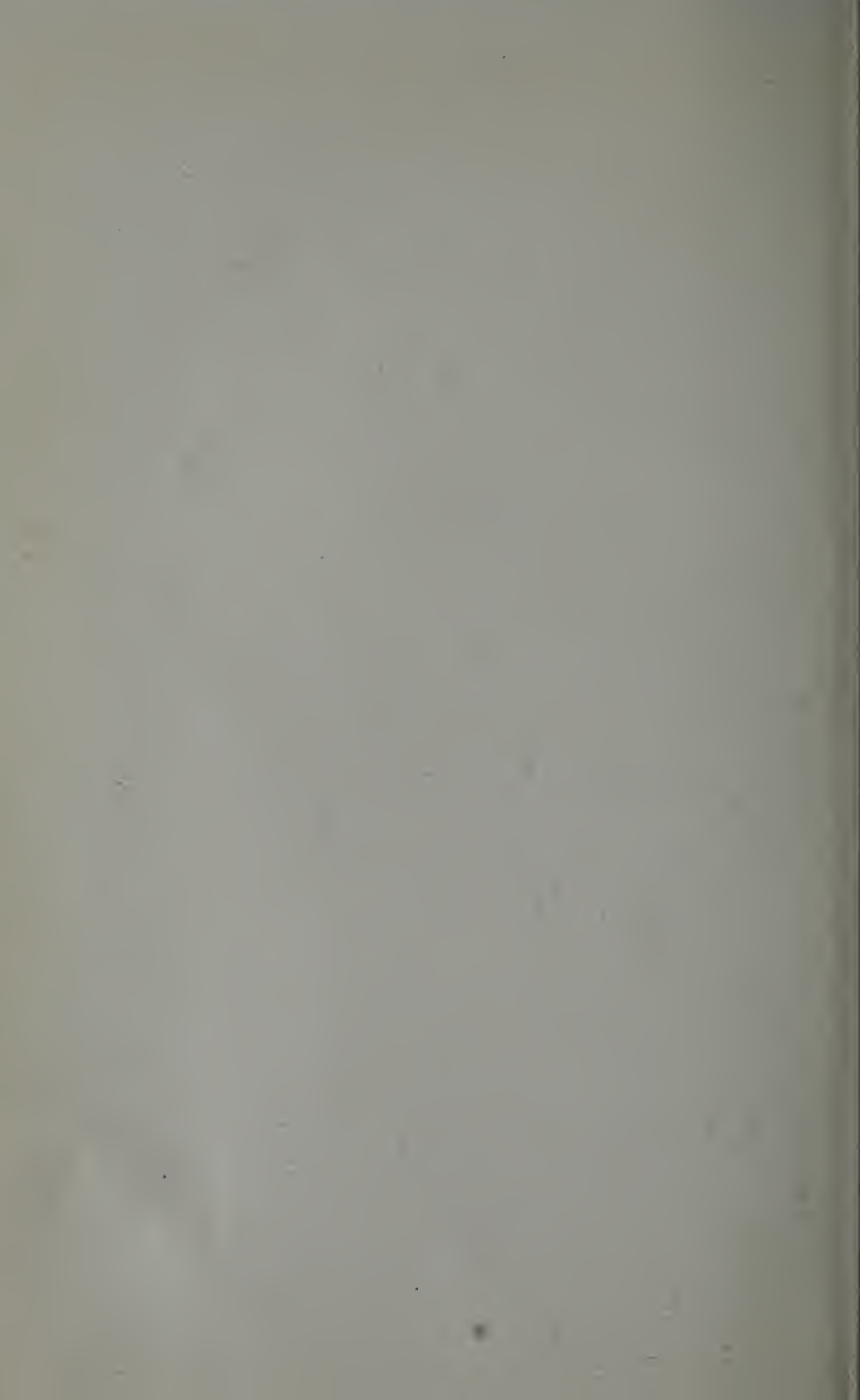
If mutations occur at random we are faced with the problem of how the type in which they occur can persist. We must admit that in order to insure persistence all the mutations occurring in a single type must be linked or complementary. A modification occurring in the dentition unaccompanied by suitable changes in skull, in musculature, in the whole organism, cannot become dominant. Thus we find in time complete specific and later generic differences profound in nature and far-reaching in influence, the beginnings of the formation of new families, new orders, new classes. As Bergson puts it there must be postulated an *original impetus* which is inherited. "This impetus, sustained right along the lines of evolution among which it gets divided, is the fundamental cause of variations, at least of those that are regularly passed on [mutations], that accumulate and create new species. In general, when species have begun to diverge from a common stock, they accentuate their divergence as they progress in their evolution. Yet, in certain definite points, they may evolve identically; in fact they must do so if the hypothesis of a common impetus be accepted."

APPENDIX

Below are cited a few of the more important recent works upon Teeth or allied problems touched upon in this volume. From references contained in these the student who desires further acquaintance with the subject will readily obtain the majority of the literature, a summary of which is considered to be beyond the scope of this introductory book.

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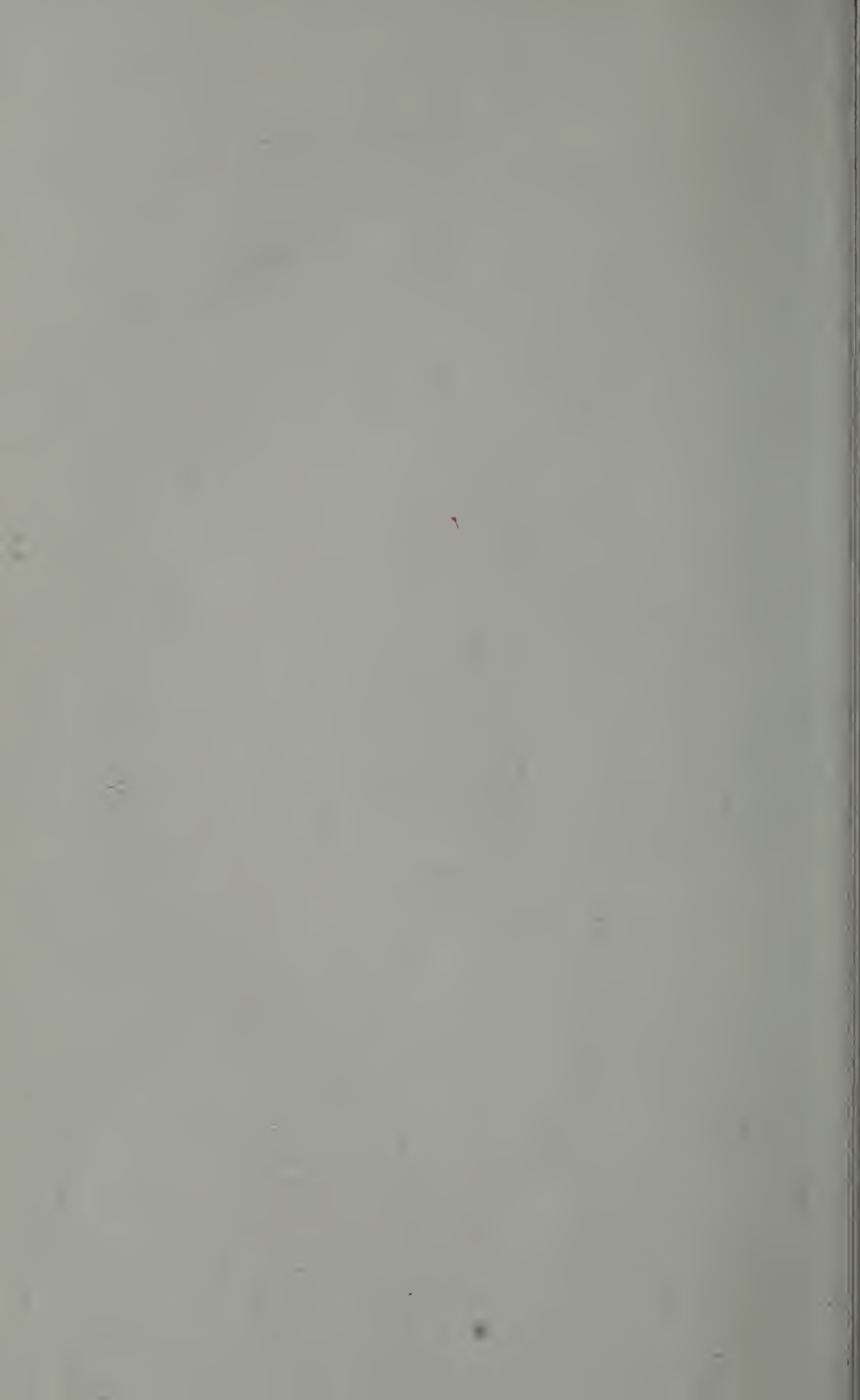
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